Chapter

Weed Seed Dormancy: The Ecophysiology and Survival Strategies

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Abstract

This chapter deals with seed dormancy of agricultural weeds, its definitions and types from the physiological and ecological point of view, and physiological and ecological factors inducing dormancy in different weed species. The role of different environmental factors, agricultural practices including herbicides application, selection pressure, and seasonal dormancy, weed density and population regulation, seed phenology, polymorphism, and modifications were emphasized. Factors induce or terminate dormancy and enhance seed germination and dormancy breaking have been mentioned and evaluated in addition to the ecological importance of seed dormancy and herbicide resistance, genetic bases of dormancy, and molecular studies were presented. The role of allelochemicals, stresses, and dormancy and their effects on seed longevity and germination regulation were thoroughly discussed. Dormancy breaking under laboratory conditions, role of plant hormones and other chemicals, and dormancy management in the field were reviewed in addition to information on seed dormancy/longevity and germination stimulants. Seed germination stimulants and inhibitors of parasitic weed and seed dormancy as a weed survival strategy were presented and discussed.

Keywords: dormancy, primary dormancy, secondary dormancy, weeds, ecophysiological factors, agricultural practices, dormancy-breaking chemicals, plant hormones, stress factors and dormancy, herbicide resistance and dormancy, dormancy management, stimulants and inhibitors, parasitic weeds

1. Introduction

Weeds represent a real persistent problem and can be found everywhere in all agricultural systems. They represent one of the main factors responsible for crop yield reductions, lower yield quantity and quality, and cause severe stresses and shortage in the supply of growth factors as they impair or negate crop yield. Losses caused by weeds exceed the combined losses resulting from insect and plant pathogens [1]. Weeds compete with crop plants for water, light, nutrients, and CO_2 under certain conditions. They harbor insect and plant pathogens and negatively affect water resources and the environment. Weeds have different life cycles and are grouped into annuals, biennials, and perennials. While perennials are mainly reproduced vegetatively, seed production is the main regenerative strategy involved in the succession of annual, biennial, and simple perennial weeds through the buildup and persistence of their seeds in the soil seed bank. Knowledge on weed seeds and their lifespan is essential for researchers as well as farmers in designing successful weed control programs. Seeds in the soil represent the passive weed population that remain viable for extended periods of time and able to re-infest agricultural lands in spite of effective weed control measures employed against both the active weed population found above the soil level and seed bank as well through certain control measures such as soil-applied herbicides, tillage, soil solarization, mulching, and flooding. Information on weed biology helps optimize weed management strategies by prediction of weed emergence time and weed infestation level and thus avoid unnecessary weed control input. Integration of knowledge on weed emergence and infestation level and seed dormancy status could be used to improve weed control strategies [2], while integrated approaches that place priority on depleting weed seed banks through interfering with dormancy or germination requirements have a strong potential to enhance weed management aspects of agricultural systems [3].

The main objectives of this study were to review the most recent advances on weed seed dormancy, highlighting the importance of weeds as the main agricultural problem, the importance of weed control and weed ecological and agricultural significance, and their importance in the agricultural system and in food production; emphasize the difficulties in weed control and challenges that the farmers face on what the weed species are possessing, role of seed dormancy in weed persistence and difficulties in weed control, role of genetic and ecological factors and their interactions, and influence of these on seed internal structure and physiology; and understand and introduce the readers to the recent findings on weed seed dormancy breaking and possible management under field conditions.

2. Importance of seed production and differences between weeds and crops

Weed seed bank is described as a reservoir at which both deposit and withdrawal operations occur. Seed production in terms of numbers is considered as a survival strategy that enables weeds to maintain their genetic lines and exist in the environment. It is important in agriculture since weeds can produce a huge number of individuals for ecological invasion and survival under unfavorable environmental conditions and thus maintain species where other regenerative propagules (e.g. vegetative organs for perennials) fail. Weeds are characterized by their huge number of seeds produced which is much higher than crop plants. These seeds are equipped with different modifications that enable their disperse far distances from mother plants to explore and invade new rich sites in growth factors and thus escape hazards in resource-depleted habitats underneath the parent plants. These modifications facilitate seed dispersal by different agents including water, wind, animals, machines, and packed agricultural materials and by man himself. However, the small-size or dustlike seeds of many noxious weed species do not require specialized agent for dispersal but can far-disperse by wind currents. In general, weed seeds are easily spread and transport from their origin, and some have found their way into the earth's planetary boundary. In order to maintain species genetic line, high seed production and seed modifications are necessary but not enough for species existence and persistence in a changing climate. Hence these characters must be accompanied with other mechanisms that help weed seeds remain viable and survive, and weeds grow and flourish in their habitats away from hazards including weed control measures. Therefore, seed production and modifications must conjugate with dormancy through which seeds of certain weed species such as *Lupinus* and *Chenopodium* can exist and remain viable for thousands of years. Dormancy is keeping seeds or buds safe until the cause of it is over. It is a significant feature contributing to weed survival rate and helps them avoid herbicides and other weed control measures along with unfavorable environmental conditions. The aforementioned weed characters are very well expressed and demonstrated when weeds also exhibit seed polymorphism, heteromorphy, or heteroblasty. Certain weed species produce different types of seeds per different plants or at different parts of the same plant, different in seed colors, structures, longevity, and more importantly germination capacity and requirements. Species of *Chenopodium*, *Amaranthus*, *Haloxylon*, *Xanthium*, *Rumex*, and many others are good examples (**Figure 1**). The ability of certain weed species to produce seeds of different colors, size, or coat characters in response to certain environmental conditions is very well documented. For instance, seeds of *Rumex vesicarius* L. are polymorphic (light and dark of various shades) and of a high potential viability [4]. Seeds are enclosed within showy, papery fruiting valves at maturation. Naked seeds exhibit non-deep physiological dormancy and usually require an after-ripening period for several months, after which they can germinate at any time of the year in a light-dark period. Light seeds are nondormant and show excellent germination in constant darkness; dark seeds are inhibited in darkness but not in a light-dark rhythm. The conditional dormancy of dark seeds is due to the pericarp that may restrict oxygen consumption by the embryo, contain chemical inhibitors, and/or impede radicle protrusion. A range of environmental variables is likely to affect the specific germination requirements of particular seed types. However, environmental conditions may induce secondary dormancy, in both light and dark seeds [4]. *Cirsium arvense* (L.) Scop. ecotypes showed differences in seed germination and in reproduction methods at different temperatures: one ecotype tends to reproduce vegetatively at high temperature (37°C), while the other is reproduced by seeds at low (17°C) temperature [5]. Pre-chilling releases seed dormancy of this species. Creeping thistle seeds did not show any apparent endogenous seasonal dormancy. Environmental conditions in the soil seed bank resulted from variations in germination. Dormancy was completely broken when imbibed seeds were stored for 2 months at 19°C, but at longer storage periods, dormancy was developed. Dormancy breaking at lower temperatures was slower and incomplete. Nitrate, desiccation, and light effects on seed germination were season-related.

In summary, prolific seed production, seed modifications, and dormancy are the characters jointly considered for a successful efficient weed species. These, however, are all absent in crop seeds hence exposed to different breeding programs resulting in loss of many characters that enable them to survive and tolerate harsh conditions

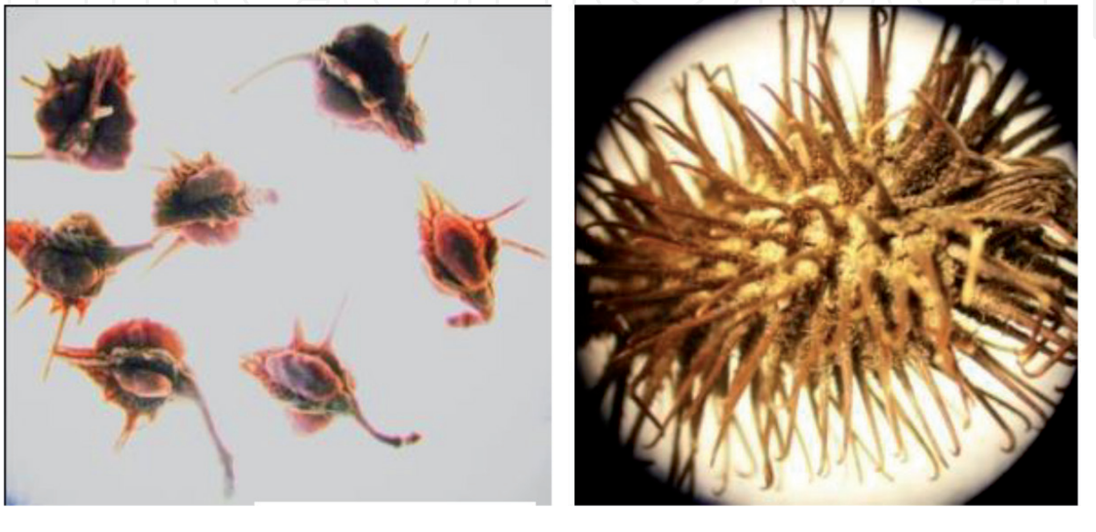

Figure 1.
Rumex acetosella L. (left) and Xanthium strumarium L. (right) fruits showing modifications on fruit case.

including plant disease, salinity, and drought resistance, and thus most crops lost their seed modifications and dormancy. Cultivated crops are well selected, and their seeds do not possess dormancy [6]. Therefore, the time of emergence and the number of established individuals could be simply determined by environmental factors (mainly temperature and moisture) [7, 8]. In contrast, prediction of weed seed germination and their emergence capacity are not possible because of dormancy. The number of established weed seedlings is strongly dependent on the dormancy level of the seed bank, and the emergence time depends largely on the seasonal dynamic variation in seed bank dormancy [9]. In addition to the mentioned characters, weeds continue producing seeds throughout their life cycle, set seeds at all growth stages, have seeds of different stages on the same plant, and show seed polymorphism.

3. Factors cause seed death in the soil

Upon the fall of mature seeds on the soil, these may be deeply deposited or remained on the soil surface and thus exposed to different climatic conditions including light and air temperature or to agricultural practices such as tillage, hoeing, or herbicides. Seeds on the soil surface may be inserted in the top soil layer 2–5 cm depth which is applied to seeds of most weed species and could be of great value facilitating rapid germination especially photoblastic species that require light for germination, or small seeds contain small food reserve. In addition, surface-laid seeds are liable to drift by wind currents or water erosion or disperse by different agents to new regions and thus avoid suffering from depleted resources under or in the vicinity of their parent plants giving them a survival value. Other soil-deposited seeds remain in full darkness and may be at different soil depths. These either germinate in full darkness or stay dormant if it requires light until brought to the soil surface by deep tillage. However, the ability of different species to emerge from different soil depths depends on their seed food reserve whether it is sufficient to support the seedling travel along the soil way distant or not. Some may consume all food storage before its emergence above the soil, and thus their growth is arrested during transit and dies. When conditions do not permit seed germination in the soil, seeds remain dormant, viable, and ready to germinate when these permit. The longevity of these seeds depends on the stored food and microbial attack of these in the soil. Other factors cause seed death including enzyme action and oxidation that denatures seed-stored food, protein coagulation, nuclei degeneration, and accumulation of toxic materials. In addition, seeds may be attacked by earthworms that collect weed seeds and move them into their burrows, while soil insects such as carabid beetles are voracious eaters and can consume a large quantity of weed seeds that drop into the soil.

4. Types of weed seed dormancy

Seed is simply defined as a fertilized egg produced after pollination, but apomixes, autogamy, and agamospermy also exist in certain weed species. The seed has been also defined as a ripened ovule consisting of an embryo and coats [10]. The embryo as the new plant in miniature is very well equipped structurally and physiologically for dispersal, has enough stored food that provide the growing seedling at early stages after emergence and until establishes itself for autotrophic organism or partially or completely dependent upon other plant species in case of some parasitic species (hemi- or holo-heterotrophic).

Dormancy in a general term is a state in which viable seeds, spores, or buds fail to germinate under favorable conditions of moisture, temperature, and oxygen for the seedling growth. It is referred to as an adaptive feature that optimizes the distribution of seed germination over time. It characterizes many weed seed populations; and this hampers efforts in predicting timing and extent of weed emergence. Indeed, the number of established plants of a weed is strongly related to the proportion of the seed bank that has been released from dormancy and the carrying capacity of the environment. Dormancy due to external conditions exerts influences on physiological and biochemical seed internal processes including enzyme activities, food transport to embryo, and metabolism or unknown internal factors or ecophysiological behavior that does not allow germination. Therefore, the causes of this status are due to the seed and its environment. On the other hand, germination involves the resumption of embryo growth and seedling emergence and growth. Germination requires moisture, oxygen, temperature, and maybe light in photoblastic seeds. Therefore, it proceeds whenever seeds are laid on a safe site to meet particular sets of environmental conditions which, presumably, are able to support not only germination itself but also to insure the survival and success of the offspring [11].

Several types of weed seed dormancy have been recognized and described under different terms as primary and secondary, inherent/genetic and environmental, innate, induced and enforced, constitutive and exogenous, and seasonal and opportunistic. Nikolaeva [12] mentioned 15 types of dormancy based on germination inhibitory and stimulatory factors. The primary dormancy (induced during seed maturation) and secondary dormancy (induced naturally or artificially following harvest) are mainly considered by most researchers.

However, based on the mechanism that causes dormancy, the following types are well recognized to occur in weeds:

1. Physiological mechanism of dormancy

2. Ecological or demographical consequences of dormancy

Both are important to understand the evolutionary adaptations that weed seeds have developed in the agricultural environment.

4.1 Physiological mechanism of dormancy

This dormancy includes the following three types.

4.1.1 Innate dormancy

Innate dormancy is also termed as a primary or genetic dormancy. It represents seed conditions when they leave parent plants in a viable state but not germinating although conditions are favorable mainly due to some property of the embryo or the associated endosperm or maternal structures. It is an inherited type that characterizes certain plant genera or families, and since genetically controlled, therefore its length depends on environmental factors. Seeds, however, will not germinate although conditions permit and dormancy period expires. The cause of such a dormancy includes a number of morphological and physiological factors, and these are as follows.

4.1.1.1 Hard seed coat

Hard seed coat that is impermeable or mechanically resists diffusion of water, oxygen, or both is also termed as physical dormancy [13]. It occurs in some or all species of the angiosperm families including Anacardiaceae, Bixaceae, Biebersteiniaceae, Cannaceae, Cistaceae, Convolvulaceae, Cucurbitaceae, Dipterocarpaceae, Geraniaceae, Lauraceae, Leguminosae, Malvaceae, Nelumbonaceae, Rhamnaceae, Sapindaceae, Sarcolaenaceae, Sphaerosepalaceae, Surianaceae, and others; but it has not yet been reported in gymnosperms [14]. Leguminosae includes approximately 800 genera and 20,000 species that are widely distributed and adapted to different habitats [15, 16] and has a high frequency of physical dormancy [17]. Some examples of these are *Lupinus*, *Prosopis*, and *Vicia* that usually show water impermeability. Species of Amaranthaceae, Chenopodiaceae, Oleaceae, and Solanaceae do not possibly allow water diffusion to dissolve and transport food to the embryo for metabolic processes. The waxy cuticle is the major impermeable barrier to water entry (polyphenols and lignifications). It was found that seed coat impermeability to water is the major reason for the persistence of velvetleaf (*Abutilon theophrasti* Medik) seeds in the soil [18], while seed dormancy of *Avena fatua* L. could be easily broken by breaking the pericarp, scarification, or abrasion by sand. However, physical dormancy is caused by one or more palisade cell layer(s) called macrosclereids [19].

Other seeds do not diffuse oxygen for energy and embryo respiration and metabolic processes. Such seeds are said to be "gas-hard," for example, *Xanthium* species, at which seed testa prevents oxygen diffusion into the embryo and thus shows undormant long seed and short dormant seed. Impermeability to oxygen may be also due to the presence of mucilage in and around the seed coat and/or the consumption of oxygen by the seed coat itself.

In the third type of seeds, both water and oxygen are not diffused through the hard seed coat such as for *Convolvulus arvensis* L. seeds that can withstand 5 years soaking in water and species of the Chenopodiaceae family.

Hard seed coat may restrict the diffusion of O_2 to enter the seed, prevents the outward release of CO_2 and/or inhibitors from the seed or embryo and also embryo protrusion and expansion, and blocks light passage to the embryo. However, seed coat and other structures surrounding the embryo are extremely important for seed survival and germination regulation, since they protect the embryo against external hazards and regulate germination time.

In other cases, seed dormancy in many species is imposed by the structures surrounding the seed. In addition to the seed coat or testa, these also include the pericarp, glumes, palea (hull), and lemma in cereals. The palea, lemma, and pericarp are responsible for coat-imposed dormancy in *Avena fatua*. These may prevent water uptake and gaseous exchange, thus responsible on insufficient availability of oxygen to support the level of respiration needed for germination or to oxidize inhibitors. They contain chemical inhibitors in the seed cover that inhibit germination process or may prevent leaching of inhibitors from the seed. These structures also modify light reaching the embryo and blocking light penetration to the embryo and act mechanically to constrain embryo expansion. In *Datura stramonium* L. seeds, both the endosperm and to a lesser extent the testa impose dormancy on the embryos, hence restricting radical growth. Removal of the testa did not improve germination, but removal of the endosperm and testa enhanced germination, similar to soaking of seeds in gibberellic acid or benzyladenine solutions [20].

In order to enhance seed germination, seed coat must be destroyed mechanically or by microorganisms. However, in legumes the seeds are hard with thick-walled cells of testa surrounding the waxy layer.

In other cases seeds may fail to germinate because of mechanical resistance of the seed coat which can withstand a high pressure of 1000 Psi, such as for seeds of *Amaranthus retroflexus* L., *Brassica nigra* (L.) W.D.J. Koch, and *Capsella bursa-pastoris* (L.) Medik. *Clavaria major* C.F. Gaertn is another example at which hard pits require 623 kg to break.

In these species, the passage prevention or difficulty of water and oxygen inside the seed is not the cause of germination failure but may be enhanced to germinate by partial digestion of seed coat by animals and thus overcome their dormancy otherwise they extinct. Germination of many weed species was greatly improved after it passed through the digestive systems of animals and dropped out with animal feces mainly because their hard coat became lenient by secretions from the digestive system of these animals.

4.1.1.2 Presence of endogenous inhibitors

These are allelochemicals that prevent seed germination and cause self-inhibition (autopathy). Chemical inhibitors may be found on seed coat or its associated structures. *Chenopodium* spp., *Lactuca*, and *Beta* seed coats contain inhibitory chemicals. Inhibitors are also found in the embryo, cotyledons, endosperm, and some inside the seed. The outer coverings may prevent leaching of these inhibitors. However, when the embryo is isolated and placed in water, the inhibitor is leached out, and germination occurs as found in wild oat (*Avena fatua*) and *Xanthium* species.

The perianth associated with the seed coat of *Chenopodium murale* was the cause of its germination inhibition. Water leached from the perianth inhibited seed germination of wheat and barley [21], while water leached from the perianth-scarified seeds had no inhibitory effect on both crops. Inhibitors are also found in structures associated with the seed coat of *Chenopodium album* L. However, the period of effectiveness of these inhibitors depends on their stability. Removal of inhibitors may be achieved by placing seeds under running tap water or in irrigation channel in the field and thus washing off water-soluble inhibitors.

4.1.1.3 Control by biochemical trigger

In this case seeds need to be biologically stimulated. The photoperiodically operated triggers act through modification of the phytochrome system. Seeds of *Betula pubescens* Ehrh. require light and long-day photoperiod for successful germination. Dormancy breaking requires light and dark stimuli and also temperature stimuli. The effect of temperature on the rate of dormancy induction is not only dependent on prevailing temperature but also on temperature experienced by seeds during previous dormancy release and the resulting dormancy status of the seed population [22].

Chilling or temperature fluctuation may be also important. In two populations of *Papaver aculeatum* Thunb. exposed to temperature fluctuation, seed dormancy was weak, and fresh seeds germinated to nearly 100% at 20/10 and 25/15°C day/night if provided with light and up to 50% at 15/5°C, but germination was prevented at 30/20°C [23]. In another study, Dahlquist et al. [24] reported that six different weed species of different families showed different tolerance to lethal levels of high temperature and responded differently to germinate at different temperature regimes; however, temperatures of 50°C and above were lethal for seeds of all species.

Germination stimulants may be used under laboratory conditions but have little relevance to field situation. Gibberellins, thiourea, or nitrate ion in the soil solution could increase with soil temperature in the spring and thus could stimulate seed germination of *Chenopodium album* and *Avena fatua*.

4.1.1.4 Immature or rudimentary embryo when the seeds are shed

Embryo dormancy is defined as failure of a mature embryo to germinate or to grow even when isolated from the seed or dispersal unit and exposed to conditions favorable for growth. Embryo dormancy may be also exerted by cotyledons as for *Fraxinus* species seed that needs removal of the cotyledons or part of them to break the embryo dormancy. However, in this kind of dormancy, mature seeds of certain weed species are not able to germinate after leaving parent plants because the embryo is not fully developed. Seeds at this stage are physiologically immature when left by mother plants. For some weed species, the seeds require an after-ripening period for the embryo to get mature, and this requires in some cases changes in hormone contents or translocation of stored materials. Afterripening is the loss of dormant state over a certain period through exposure of seeds to a set of environmental conditions after maturation and separation from the parent plant [25]. The after-ripening process, however, occurs during a period of dry storage of freshly harvested mature seeds and is essential in releasing dormancy and in promoting germination [26, 27]. However, dry conditions are not always the case required, but plant species vary in environmental conditions that facilitate afterripening, while wild oat seeds after ripening under warm, dry conditions, and *Arabidopsis* and many other species respond best to cool, moist conditions [28, 29]. Seeds of *Acanthospermum hispidum* A.P. de Candolle that born immature and grow after the seed is shed and those of *Heracleum sphondylium* L. require several months after shed. Seeds of *Orobanche* spp. require a conditioning period of 3–4 months during which the embryo is mature enough to respond to host germination stimulants. This status, however, is overcome when embryo growth is complete.

Other weed species exhibit polymorphism and produce morphologically and physiologically different seeds that have different after-ripening periods such as for seeds of *Xanthium strumarium* L.

Several mechanisms sometimes may operate together in a single seed to break innate dormancy. For example, seeds of *Galium cracoviense* Ehrend. require lower Ca^{2+} ion concentration, moderate temperatures, and presence of light to germinate [30]. Garden cress (*Lepidium sativum* L.) seeds only germinate in response to a combination of light and temperature, while seed germination of *Chenopodium album* requires treatment with red light, cool temperature, and nitrate. The desert annual weed, *Trigonella arabica* Delile, has a dispersal unit equipped with at least four operating dormancy controls including water-soluble inhibitors, hard seed coat, sensitivity to light, and temperature.

Sometimes overcoming dormancy may be highly specific and adapted to certain conditions. Seed germination of *Rhus* spp. and *Epilobium angustifolium* L. and seedling growth occurred after forest fire that causes a waterproof layer of the dispersal unit to become permeable. Dormancy breaking may be also controlled by rain and temperature since there is an optimum levels of both to germinate.

Cold temperature may be required for germination of certain species; it could activate hormones and enzymes. Some seeds need exposure to alternating temperature between freezing degrees for several weeks to one or two exposures to high temperature. This temperature fluctuation causes heat shock and activates enzymes and hormones and enhances their mobilization and thus germination induction as the treatment for *Lithospermum arvense* L. seeds. However, many chilling requiring seeds do not show hard seed coat. Temperature can affect both germination and dormancy. At minimum and maximum temperatures, germination does not occur with some exceptions, while each weed species has an optimum temperature at which it germinates. Lower or higher than that germination is affected until totally prevented at extreme temperatures. *Amaranthus* sp. remains dormant at 20°C for 6 years, while raising the temperature released its dormancy breaking.

Light is another regulatory factor of seed germination for certain weed species having a light requirement (photoplasts) before the start of germination. Light-stimulated germination of seeds is known to involve the phytochrome system. The photoconversion of red light (P_r) to far-red light (P_{fr}) stimulates germination.

Lactuca sp. is a good example on light requirements for dormancy breaking. Seed germination occurs within a narrow temperature range, but giving light the seeds germinate promptly and uniformly over a wide range and under a variety of conditions that would inhibit germination in the dark. Dry seeds of *Lactuca* are insensitive to light, but when moistened and exposed to few foot candles for a few seconds, this treatment had a full effect on seeds. Moistened light-treated seeds retain their ability to germinate when dried and restored, but when subsequently remoistened, they germinate in darkness. However, the brief exposure to light that stimulates germination of *Lactuca* seeds is not enough for *Juncus maritimus* Lam. seeds to germinate. Continuous illumination works well with *Lactuca* but would inhibit seeds of *Atriplex rosea* L. plant that is fully stimulated by a brief exposure.

Sensitivity to the period of light and dark may determine the season of germination and growth, the flower initiation, and the end of bud dormancy. However, the value of light in stimulating or inhibiting seed germination may be very well demonstrated on species survival and existence knowing that germination inhibition by high light intensity may be of value in preventing germination and growth of winter weeds during the summer time at which soil surface may be exposed to unfavorable conditions such as drying or rapid seedling desiccation due to high temperature, high light intensity, and long photoperiod during summer and unsuitable for winter weeds. Conversely, germination inhibition of summer weed seeds during winter prevents their possible death by freezing temperature, strong cool wind currents, short photoperiod, and low light intensity which are not in favor of summer weed growth and survival. This kind of inhibition caused by light on the two weed groups of different growth requirements is a good example on the important value of light inhibitory effects for the survival of these species. However, seeds of many summer annuals at low temperatures under moist conditions provoke dormancy release, while high temperatures induce secondary dormancy. The seed dormancy level establishes the range of temperatures under which germination is possible [22].

4.1.2 Induced dormancy

It is an acquired condition of inability to germinate caused by some experience after ripening. This kind of dormancy is also called secondary dormancy as seeds are ready to germinate but may go into dormancy due to sudden changes in environmental conditions such as in temperature, moisture, and oxygen levels that cause physiological changes in seeds. Seeds, however, will not germinate, and dormancy exists even when conditions changed to favorable. This dormancy may be resulted from seed exposure to excessive light which lead to no germination in darkness, lack of moisture, high CO_2 pressure, low O_2 pressure, and deep seed burying that will not germinate until they are brought to the soil surface. However, other buried seeds by tillage may not germinate even after they are brought to the soil surface.

4.1.3 Enforced dormancy

This kind of dormancy is maintained in or on the soil or with seeds submerged in water. It is defined as the inability of seeds to germinate because of environmental factors. One or more factors necessary for germination are in a short supply or absent including the lack of moisture, low temperature, lack or low oxygen level, and poor aeration and unfavorable atmosphere. However, percentage of O_2 found in the soil depends on soil porosity, depth, presence of microbes, and amount of soil moisture. When the external limitation is removed as seeds are brought to the soil surface by tillage, they germinate. Sometimes this dormancy is due to placement of weed seed deeper than 5 cm in the soil by tillage. It results from the absence of red (r) light under the soil surface. Red light induces germination in seeds by activating their phytochrome system (P)-chromophore blue pigment attached to the protein molecule in the seeds. Far-red (Fr) light deactivates the system and thus induces dormancy in weeds. However, dormancy does not persist when the environment changes.

Both induced and enforced dormancy make the secondary dormancy. The importance of secondary dormancy became clearer as a survival strategy prevents seed germination when seeds are found deep in the soil and seedlings will not be able to emerge from deep soil layers. This kind of dormancy may be regulated through the phytochrome pigments found at low concentrations inside the seeds. These pigments when exposed to a high percentage of P_r/P_{fr} induce germination. The exposure time may be short enough for parts of the second dormancy. However, seeds from a single weed species may exhibit one or more types of dormancy or all three in succession over a period of time. Primary dormancy is found in the freshly shed seeds at which they will not germinate under any environmental conditions until dormancy is broken. After primary dormancy breaking, the seeds may germinate providing that conditions are favorable. If suitable external factors are not present, then secondary dormancy may develop. Secondary dormancy can be relieved and re-induced during many successive years [31] until conditions for germination become favorable. This phenomenon is called dormancy cycling [32]. However, physiological differences between secondary and primary dormancy are unclear [33].

From the ecological point of view, seed dormancy is also termed as a dispersal by time and is defined as an arrest in the development of seed embryo under external environmental conditions suitable for plant growth (phase more resistant to environmental hazards). It is critical for annuals not perennials. However, two approaches are prevalent, and these are as follows.

4.2 Ecological and teleological dormancy

Dormancy from an ecological perspective is defined as a seed characteristic that prevents germination, even if suitable germination conditions prevail, not involving embryo or seed morphology or germination mechanisms. This is either as follows:

4.2.1 Seasonal dormancy

This kind of dormancy occurred at which favorable factors for germination were found but seeds of certain plant species have winter or summer dormancy. It occurs in an environment where favorable growth conditions are seasonal and dormancy is usually clocked by solar rhythm. This is applied to all annual summer and winter weeds at which day length is important, while temperature may not be so if followed by cold weather. Day length is the best indicator of seasonal changes because it is a rather constant feature of the macro-environment. The disadvantage of seasonal dormancy is that seeds may not be developmentally advanced enough to take advantage of especially good spring or summer conditions. If the environment is not stable (rainfall in the desert, fire, soil disturbance), it may make conditions favorable for seedling growth, but the timing and duration of these events can be rather unpredictable.

Differences were found among populations of *Solanum nigrum* L. collected on two dates from different locations. Fresh seeds were conditionally dormant and germinated at higher alternating temperatures and in light, while seeds of *Solanum physalifolium* Rusby were deeply dormant. Seed dormancy is reduced during autumn, winter, and early spring in soil-buried seeds. The rate of dormancy release and induction is low at lower temperatures and increases as the temperature rises. High temperatures cause short-lasting breakage of dormancy followed by induction.

Seedling emergence of both species showed a bi- or three-modal pattern during an extended period in late spring and early summer. This enables the species to survive natural catastrophes or escape weed control operations. Dormancy is mainly induced during summer due to higher temperatures. This prevents seedlings from emerging too late and being killed by frost in autumn before reproduction [34]. Kołodziejek and Patykowski [35] reported that *Rumex confertus* Willd. Germination percentage and rate were significantly higher in light than in darkness. Seeds incubated for 12 weeks in the dark at 4°C exhibited secondary dormancy. Weed seeds undergo a seasonal deep dormancy in winter and early spring and a low level of dormancy in early autumn. Germination, however, decreased with soil salinity, while NO_3^- enhanced speed germination. Seeds burying at >0.5 cm reduced germination.

4.2.2 Opportunistic dormancy

In this kind of dormancy, seeds of certain species are able to take advantage from unpredictable environmental conditions or changes. It occurs when there is only a small seasonal element in the occurrence of favorable conditions; dormancy tends to be both imposed and released by the direct experience of the unfavorable or favorable conditions. For instance, deep tillage brings the seeds to the soil surface and thus would allow successful germination and establishment. Ephemerals in the desert sometimes take an advantage from the sudden rain shower during summer at which they germinate but later they suffer death because of the usual prevailing conditions of drought and high temperature in the desert during that period.

The advantage of seasonal dormancy is its predictable nature, while the advantage of opportunistic dormancy is its responsiveness. The differences between the two types are not exclusive but changed when conditions are changed. However, physiological description of dormancy may be a more valuable approach since the conditions of the embryo are what finally determine seed germination.

5. Physiology of dormancy in weed seeds

Dormancy is an adaptive trait that enables seed germination to coincide with favorable environmental conditions. From the physiology perspectives, gibberellins, ethylene, cytokinins, or abscisic acid (ABA) play an important role in inducing or inhibiting seed dormancy. The low level of ethylene is accumulated at the early stage of germination in seeds of different crops (e.g., *Ricinus communis*, *Lactuca sativa*, *Hordeum vulgare*) and weed species (e.g., *Avena fatua*) just prior to radical protrusion. Nondormant *Xanthium pensylvanicum* embryos produce more ethylene than dormant seed. Cytokinins increased in dormant seeds of *Rumex obtusifolius* and *Spergula arvensis* during dormancy breaking and chilling periods. On the other hand, ABA application inhibits seed germination. It has been suggested that related or common receptors for dormancy-breaking agents are present within the plasma membrane of the responsive embryonic cells. When triggered, these receptors initiate a signal transduction cascade, perhaps involving synthesis of or sensitization to germination-promoting gibberellins (GAs) that complete germination. Changes in the phosphorylating activity of membrane-associated, Ca^{2+}-dependent protein kinases that lead to dormancy or germination have been also proposed.

There is considerable circumstantial evidence that ABA is involved in regulating the induction of dormancy and in maintaining the dormant state. However, there is a paucity of unequivocal evidence that ABA is in fact an important controlling factor in the dormancy of most seeds. Dormancy is induced by abscisic acid during seed development on the mother plant. After seed shed, germination occurs due to reduction in the ABA level of the imbibed seeds because of ABA catabolism through 8-hydroxylation. ABA/gibberellins balance is the main environmental factor responsible for inducing or breaking seed dormancy. However, in different species, ethylene counteracts ABA inhibitory effects and stimulates germination. This effect is very well demonstrated in Brassicaceae seeds, which counteracts ABA effects on endosperm cap weakening, facilitating endosperm rupture and radical emergence. In contrast, ABA limits ethylene biosynthesis and action. Nitric oxide has been proposed to act against ABA inhibitory effects on ethylene and hence is produced rapidly after seed imbibitions and promotes germination by inducing the expression of the ABA 8-hydroxylasegene, *CYP707A2*, and stimulating ethylene production. The role of nitric oxide and other nitrogen-containing compounds, such as nitrate, in seed dormancy breakage and germination stimulation has been reported in several species. Both ethylene and nitric oxide have been shown to counteract ABA action in seeds, improving dormancy release and germination [36]. Abscisic acid has been also found to inhibit RNA synthesis. In seeds of *Chenopodium album*, ABA has been found to inhibit the embryo growth necessary to penetrate the coverings of the seed, although the initial events of embryo expansion are not prevented [37]. ABA deficiency was found to associate with the absence of primary dormancy, while high ABA content could promote seed dormancy. ABA is synthesized in the embryo and endosperm, and the balance between GA and ABA determines dormancy in weed seeds. GAs are known to obviate the requirement of seeds for various environmental cues, promote germination, and counteract the inhibitory effects of ABA, frequently in combination with cytokinins.

From the above information, it becomes clear that some plant hormones have roles in dormancy induction or breaking and thus inhibit or stimulate seed germination. Ethylene stimulates seed germination of several weeds such as in *Avena fatua*. Gibberellins increase in seeds, require stratification, and also facilitate degradation of food reserves in the endosperm or cotyledons necessary for germination.

Some chemical compounds or secondary metabolites are also known as allelochemicals such as phenolics, unsaturated lactones, short-chain fatty acids, coumarins, and many others have been reported as germination inhibitors present in seeds of many weed species [38, 39]. To enhance germination, leaching and oxidative destruction of these chemicals within the seed are necessary for dormancy termination. However, these allelochemicals may also play a positive role in seed viability and longevity since they prevent microbial attack and maybe destruction of weed seeds by soil pathogens and insects.

Ecological factors are involved in inducing dormancy or stimulation of seed germination and dormancy breaking. These factors include light, temperature, O_2, CO_2, and nitrate. Light causes weed seed dormancy. Some weed seeds require light in order to germinate, for example, *Galinsoga parviflora* Cav., *Portulaca oleracea* L., *Chenopodium album*, and *Amaranthus* spp. breaking dormancy is related to light that exists in promoting and inhibiting forms. Promoting form is favored by red light and inhibiting form by far-red light. Pigment generally initiates germination when in far-red light around 750 nm absorbing form and either prevents or has no effect on germination when in the form of red light around 660 nm. The inactive form (P_r) and red light, 650 nm, resulted in germination promotion, while the active form (P_{fr}) and far-red light, 750 nm, cause germination inhibition. Leaf canopy suppresses germination through shading effects since it promotes relatively low-red to far-red photon flux ratio, producing relatively low P_{fr} to P_r ratios in underlying seeds which inhibit seed germination. Great variations do exist between weed species in pattern of development of photoplastic properties.

However, light, moisture, temperature, and O_2 all act physiologically in enhancing or ending dormancy. Moisture or water is required to activate enzymes, compensate for water loss by the embryo through respiration, and dissolve and mobilize food into the embryo. Oxygen is necessary for aerobic respiration to provide energy for embryo growth, while water absorption, hormonal balances, metabolic processes, and germination induction will not proceed but only at certain suitable temperature. All factors, however, are required for biochemical and physiological activities that occur inside the seed including the living embryo.

6. ROS production and sensing in seeds

Reactive oxygen species (ROS) play an important role in seed life cycle. In orthodox seeds, ROS are produced at all stages in seeds active cells as well as in dry tissues during after-ripening and storage. ROS, however, are widely regarded as detrimental to seeds, but recent research results reconsider them as beneficial in seed germination and seedling growth. ROS regulate cellular growth, protect against pathogens, or control the cell redox status. They also act as a positive signal in seed dormancy release by interacting with plant hormones such as in transduction pathways of abscisic acid and gibberellins [40]. Different workers emphasized ROS roles in plant physiology and development under stress conditions mainly drought stress, and thus their production has been long considered as detrimental since it is linked with seed aging or seed desiccation, but they have also a positive important role in seed germination or dormancy release. They are important in metabolic activity during cell division, seed filling, seed survival at shedding, and seed rehydration and germination. ROS have an essential role in plant metabolism, energy production, and enzyme activities necessary to start seed germination and seedling growth. Their sensing and signaling role in seed different stages is evident. ROS is important in cell signaling in the dry state since it could accumulate during dry storage but would become actors of cell regulatory mechanisms only after seed imbibition. Oxygen is important in the guise of reactive oxygen species in further modulating dormancy and relaying environmental signals. Seed dry after-ripening is associated with the accumulation of ROS, resulting in targeted mRNA oxidation and protein carbonylation of transcripts and proteins associated with cell signaling (mRNA) and protein storage [41]. These modifications have been linked to dormancy changes during after-ripening and could underpin a mechanism indicating the passage of time. Recently the possibility of a further role for ROS to inform the seasonal response of the seeds through ultra-weak photon emission (UPE) has been suggested. It was hypothesized that beneath the soil surface the attenuation of light (virtual darkness: low background noise) enables seeds to exploit UPE for transducing key environmental variables in the soil (temperature, humidity, and oxygen) to inform them of seasonal and local temperature patterns.

7. Seed dormancy in response to stresses and herbicides

Seed germination is affected by many environmental factors, such as temperature, salt, light, soil moisture, oxygen concentration, and Ca^{2+} ions. Dormancy is a status to avoid and resist adverse conditions and must be evolved as a solution to the periodic, as well as nonperiodic, changes in the environment which impair the proper function of the plant during certain periods [42]. It may also prevent germination under apparently normal conditions, if they occur occasionally. In this way, it constitutes an evolutionary safeguard against the uncertainty of the environment. Drought, salinity, alternating temperature, photoperiod, burial depth, nitrates, nitrites and soil pH, artificial seed aging, agricultural practices, control methods, and radiant heat all influence weed seed dormancy.

Studies in controlled environments have already demonstrated that thermal conditions and, to some extent, water availability during seed set and maturation have an impact on the level of dormancy [43]. The level of dormancy in *Alopecurus myosuroides* Huds. seeds depends on the magnitude and timing of temperature and water availability during the reproductive growth phase. Water availability seems more important during maternal environmental perception and temperature during zygotic environmental perception [43]. Both temperature and soil moisture content are important factors in seed germination induction. Maximum (68–100%) and rapid (2.58 days) seed germination of *Calotropis procera* (Aiton, W.T. Aiton) occurred at 30°C but declined under water stress with increasing temperature, from 92.5 ± 1.1% at 20°C and 0 MPa to 2.8 ± 1.7% at 40°C and −0.4 MPa, respectively. Seeds were unable to germinate at ambient temperatures ≥40°C but remained quiescent and viable. Planting depth also influenced seedling emergence and water stress inducing a reduction in optimum germination temperature from 30 to 20°C. Short mean germination times increase seedling survival by rapid transition from endosperm resources to photosynthesis, whereas seed quiescence (cf. dormancy) optimizes germination opportunities in a semi-arid environment. Thus, the germination traits are likely promoted seedling survival and its spread [44].

Velvetleaf seeds germinated over a range of constant temperatures from 10 to 40°C regardless of light conditions, but no germination occurred at temperature below 5°C and beyond 50°C. Seeds germinated at alternating temperature regimes of 15/5–40/30°C, with maximum germination (>90%) at alternating temperatures of 40/30°C. Germination, however, was sensitive to water stress, and only 0.4% of the seeds germinated at the osmotic potential of −0.4 MPa. There was no germination at 0.6 MPa. Germination was also reduced by salinity and alkalinity stresses and did not occur at 150 mM NaCl or 200 mM $NaHCO_3$ concentrations. However, pH values from 5 to 9 had no effect on seed germination. The maximum seedling emergence (78.1–85.6%) occurred at 1–4 cm depth [45].

Bochenek et al. [46] reported differences between the cultivars of *Brassica napus* L. seed in their potential to exhibit secondary dormancy following environmental stress. A significant number of differences in gene expression between the cultivars were apparent in the transition from full-size embryo to mature seed. Most differences were apparent in the desiccation stage, and some were in genes related to signaling processes and protein biosynthesis. Authors suggested that the propensity of *Brassica* seeds to manifest secondary dormancy may be determined by changes in gene expression that occur during late seed development [47].

Breaking primary dormancy of achenes in *Cirsium arvense* only took place during the first stratification month at moderate temperature, which is mainly due to an increase in the average water stress tolerance in seed population. The induction of secondary seed dormancy during after-ripening at all temperature resulted mostly from a substantial loss of the seed's ability to tolerate water stress [46].

The effects of drought and herbivory on biomass and seed quality in *Vaccaria hispanica* (Mill.) Rauschert have been also studied by Cici [48]. The maternal water stress suppressed seed mass but stimulated seed dormancy in seeds. Progenies from the maternal stress environment were more persistent than those from the maternal control environment after being exposed to 45°C and 100% RH for 8 days.

Nassella trichotoma Hackel ex Arech. was identified to be a non-photoblastic, with germination percentages being similar under alternating light and dark and complete darkness conditions [49]. With an increase of osmotic potential and salinity, a significant decline in germination was observed. *N. trichotoma* seed dormancy break can be triggered by favorable alternating temperatures of approximately 25/15°C and ample water availability. Radiant heat has a positive effect on total germination. Osmotic stress and salinity significantly reduced germination, while water appeared as the most important limiting factor in germination. Soil pH is not a limiting factor on this species recruitment. Herbicide-resistant populations of the same weed species have been studied to identify differences in important environmental factors on its seed dormancy. The increase in osmotic potential and salinity caused a significant decline in germination. The pH had no effect on germination. Exposure to a radiant heat of 120°C for 9 min resulted in the lowest germination in the first population (33%) and in the second population (60%). In the burial depth treatment, both populations had the highest emergence of 1 cm depth. However, variation between the two populations was observed for the burial depth of 4 cm. Differences between populations were found in emergence and overall germination [49].

Seed germination of the salt-tolerant species, *Salicornia europaea* L., that produces dimorphic seeds of high salt tolerance limits has been studied by Orlovsky et al. [50]. Germination of large seeds was found to be 3–4 times higher than of small seeds under control and at 0.5–2% of all salts tested. Germination and plant growth in mixed sulfate-chloride salts were distinctly higher than in pure chloride salts; small seeds exhibited deep innate dormancy but stimulated by 0.5–2% of chloride and sulfate salts. Small seeds develop earlier, are more dormant, and are less salt-tolerant than large seeds. Seed dimorphism made the species more flexible in its response to varying salinity and more adapted to salt and temperature stresses.

GA_3 at concentration of 400 ppm strongly stimulated germination of *C. bursa-pastoris* at 12/12 h of light/dark and continuous darkness. While KNO_3 at 2 mmol had no effect on germination, long wet pre-chilling enhanced germination. Seed germination occurred at 10–30°C and within a range of pH of 3–11. On the other hand, drought and salt stress strongly inhibited germination, but authors suggested that weed seeds can germinate at high salinity. Sowing depth is critical for germination, and seedling emergence decreased with sowing depth. The rates of *C. bursa-pastoris* germination and seedling emergence were highest for seeds on the soil surface [38].

8. Dormancy and agricultural practices

8.1 Tillage

Tillage exposes seeds to light before reburial, allows greater diffusion of oxygen into and carbon dioxide out of the soil, buries residue, and promotes drying of the soil, thereby increasing the amplitude of temperature fluctuations and promoting nitrogen mineralization. These factors are known to terminate dormancy in several species. The effects of burial, however, on germination and longevity and of water stress and temperature on germination and dormancy induction of the weed *Sinapis arvensis* L. showed that soil-buried seeds exposed to high temperatures in summer broke dormancy [51], but low water potential and constant supraoptimal temperatures induced secondary dormancy. The threshold temperature for dormancy induction was about 19°C when water was available but decreased with reduced potential. Dormancy induction increased with burial depth and was induced to its highest level (96%) at a depth of ≥5.19 cm. Water stress or more burial depth can promote induction of seed secondary dormancy.

Tillage effects on seed dormancy of different weed species are very well demonstrated especially on photoblastic species. Tillage may affect P_{fr} and P_r ratios and germination induction or dormancy. This, however, is varied for different weed species. Chavarria [11] reported that under conventional tillage, *Amaranthus retroflexus* and *Digitaria sanguinalis* (L.) Scop. seeds tend to stay in primary dormancy or develop secondary dormancy, if they become buried; further soil disturbance promotes germination since seeds are exposed to light. Lower germination is expected for buried *Chenopodium album*, *Echinochloa crus-galli* (L.) Beauv., and *Setaria glauca* (L.) Beauv. seeds, but they may overcome this dormancy without further soil disturbance. Burying seeds of *Polygonum pensylvanicaum* L., in contrast, may result in an enhanced germination after experiencing low temperatures during winter, while non-geminating seeds of this species may enter into a secondary dormancy as induced by increasing temperatures [11]. Under no-tillage systems, seeds of all species except *Polygonum pensylvanicaum* may acquire an increased germination capacity in response to exposure to conditions such as light. For *Amaranthus retroflexus*, *Chenopodium album*, and *Echinochloa crus-galli* non-buried seeds, the germination patterns may be associated with a photoperiodic response. Accelerated after-ripening occurred in seeds of all species except *Polygonum pensylvanicaum*, when stored at increasing temperatures from 0 to 40°C. *Amaranthus retroflexus*, *Echinochloa crus-galli*, and *Setaria glauca* seeds germinated better in the dark, while *Chenopodium album* and *Digitaria sanguinalis* germinated better in the light. These differences, however, were less evident for seeds stored at temperatures above 20°C, which indicates an interaction between the temperature previously experienced by the seed and its response to light conditions during germination [11].

Weed emergence was also reported as increased following frequent, repeated tillage. Cultivation during daylight serves to increase weed populations. Daytime tillage increased seedling emergence of several winter annuals and doubled that in the night time tillage due to the extreme sensitivity to P_{fr} in buried seeds of certain weed species.

Tillage modifies soil temperature fluctuations or soil nitrate concentration, and continuous tillage depletes organic matter that leads to a change in soil color and thus modifies soil thermal regime. Tillage changes the position of seeds in the soil, while no-tillage leaves most seeds in the top 10 mm of the soil profile.

8.2 Fertilization and chemical applications

Nitrates affect seeds of several species and enhanced seed germination in the field. Nitrates may influence mother plant resulting in increased nitrate level in developing seeds. A strong correlation between nitrate concentration in the seeds and their germination capacity was also found. Nitrate and nitrite concentrations have been shown to stimulate dormancy release in some species although other species are released from dormancy by ammonium. Soluble N can stimulate germination of seeds of many weeds including *Amaranthus retroflexus* and *Chenopodium album*; manipulation of soil fertility has been extensively explored as a tool for reducing weed density [3]. Practices that avoid large pulses of soluble N early in crop development, such as delayed or split N applications, or use of slow-releasing N sources, such as mature compost, can delay weed emergence and reduce weed density in the crop.

8.3 Flooding

Under irrigation and flooding conditions, the soil has low oxygen concentrations. Low oxygen concentration terminates dormancy in seeds of some species including *Echinochloa turnerana* and *Leersia oryzoides* (L.) Sw. in rice crop. Flooding, however, causes death of unadapted species and thus facilitates the establishment of *Ambrosia tenuifolia* Spreng. because of the benefits from increased R/FR ratio.

8.4 Crop residue and burning

Thick layer of residue increasingly reduces and delays emergence, decreases temperature, and prevents light penetration [3]. Soil-incorporated crop residues yield allelopathic effects on weed seed germination. Decayed residues can immobilize large amount of N that consequently prevents termination of dormancy in some species. The stimulant effect of certain plant residues is also possible. Many plant-derived smoke components have been found to have a dormancy-breaking effect, and the role of nitric oxide has been identified.

Incorporation of legume cover crop materials and application of chicken manure can promote weed emergence and growth. For example, ammonium released from decomposing *Vicia villosa* Roth can stimulate germination of *Amaranthus hybridus* L. [52]. However, the effects of N fertilization on weed emergence are varied, owing in part to complex interactions between N and other factors such as ethylene concentration in soil, light, and genetic differences in responsiveness both between and within weed species [3, 53].

9. Seasonal dormancy and shift in population germination time

Seeds of certain weed species exhibit seasonal dormancy that allow them escape hazards that occur at a certain period in the year or unsuitable environmental conditions. This phenomenon is clearly demonstrated in annual, biennial, and perennial weeds. In annuals, summer-grown weeds will not germinate during winter since growth factors are not in favor of their germination, growth, and survival; the same is true for winter-grown weeds during the summer season. This is a danger avoidance strategy. In perennial weeds such as the woody spread *Prosopis farcta* (Banks and Sol.) Macbride, it inters into dormancy by the end of fall and winter seasons, drops all leaves, and stay dormant throughout the winter season. The weed breaks bud dormancy by the start of spring and grows vegetatively throughout the spring and summer seasons. The seeds of this weed also will not germinate during dormancy period [54]. The main factors control dormancy induction, or releases in all these species are the temperature and photoperiod.

Karssen [31] stated that seasonal periodicity in the field emergence of annuals is the combined result of seasonal periodicity in the field temperature and seasonal periodicity in the width of the temperature range suited for germination. Germination in the field is restricted to the period when field temperature (environmental factor) and the temperature range over which germination is possible (degree of dormancy) overlap. So, dormancy is related to the width of the temperature range over which germination can proceed and not to temperature in that range. Dormancy varies on a continuous scale, visualized by continuous changes in the range of environmental factors under which germination can take place [55].

Seeds of the winter annual *Bromus tectorum* L. lose primary dormancy in summer and are poised to germinate rapidly in autumn. If rainfall is inadequate, seeds remain ungerminated and may enter secondary dormancy under winter conditions [56]. Maximum secondary dormancy was achieved in the laboratory after 4 weeks at −1.0 MPa and 5°C. Seeds in the field became increasingly dormant through exposure to temperatures and water potentials in this range. They were released from dormancy through secondary afterripening the following summer. Different genotypes showed contrasting responses to dormancy induction cues in both laboratory and field. The changes in $\Psi b(50)$ can be used to characterize secondary dormancy induction and loss in this weed species.

A complex nature of responses may be exhibited by *Senecio vulgaris* L. in response to intense chemical selection. Seed germination and growth normally occur during the spring season (May–April) at which heavy application of simazine herbicide is practised. The repeated application of the herbicide during this growing period forced the weed to shift its germination time and life cycle to the winter annual where no herbicide application is practised. This shift in weed germination and growth is a strategy adopted by this species to avoid phytotoxicity of the herbicide [57].

10. Seed morphology, polymorphism, and dormancy

Seed polymorphism is an important factor in innate dormancy. It is a significant factor in spreading the germination of seed from the same plant over time and keeps farmers busy with weed control throughout the whole growing season. This phenomenon is widespread in the Amaranthaceae, Compositae, Chenopodiaceae, Cruciferae, and Gramineae families.

Genetic seed polymorphism is very well demonstrated in *Spergula arvensis* L. weed. The seed coat character is genetically controlled and associated with germination. Three different seed coat forms are found in weed seeds, each controls different levels of seed dormancy; these are the homozygous papillate form bearing about 120 papillae homozygous smooth coated form, and a heterozygous form which bears 60 papillae. The papillate seeds germinate readily at 21°C, while the reverse is true at lower temperatures [58]. This is an example of genetic polymorphism which is the production of seed of divergent morphology and behavior as a result of genetic segregation. Genetically controlled polymorphism distinctly showed different dormancy genotypes.

On the other hand, certain weed species show somatic polymorphism which is the production of seeds of different morphologies or behavior on different parts of the same plant. It is not a genetic segregation but a somatic one [58]. Among weeds showing such a phenomenon are *Xanthium* spp. Fruits of these species each contain a pair of seeds large and small one deeply dormant upper seed and a lower less dormant seed [59]. Dormancy breaking is different with the result of not less than 12 months of separate germination of the two seeds which could be regarded as an obvious insurance strategy. Dormancy breaking requirements are different for the two seeds.

Placement of *Datura stramonium* L. seeds on mother plants had a significant effect on seed germination. The middle and lower seeds on the maternal plant had less germination rate and seedling vigor than those in the upper part of the plant [60].

In *Avena fatua* and *Avena ludoviciana* Durieu, the grains are born on different parts of the individual spikelet that have different germination requirements. In *Amaranthus* spp. different seeds on the same plant are produced that are different in colors and seed coat morphology (**Figure 2**). *Chenopodium album* also produces brown to black seeds. Brown/black seed production ratio is 3–97%. Black seeds require cold temperature or supply of nitrate for dormancy breaking, while brown seeds are readily germinating at low temperature and are thin-walled. However, brown seeds germinate quickly, and seedlings are killed by winter cold or agricultural operations, but if they survive, they produce very large plants with a higher reproductive output, and then black seeds germinate in the spring season. Brown seeds ripened earlier giving the same ratio of brown to black seeds which is probably environmentally governed. Brown seeds represent highly opportunistic strategy, whereas black seeds are more seasonal and predictive in behavior.

In *Atriplex heterospermum* (Greene) Nels. & Macbr weed, black seeds are produced early in the season followed by large brown seeds to avoid unfavorable conditions. *Halogeton* sp. behaves similarly at which black seeds are produced in short days, while brown seeds in long days, and the weed shows differences in

Figure 2.
Amaranthus retroflexus black and brown seeds showing seed polymorphism.

dormancy-breaking requirements. Species of the Cruciferae family show seed size and color polymorphism such as for *Eruca sativa* Mill. and *Sinapis arvensis*.

11. Seed dormancy and herbicide resistance

Under conditions of herbicide application, some of these chemicals are absorbed by seeds or dormant buds, while others are not. These result in differences in germination, emergence, and growth patterns of different weed species. However, some herbicides may stimulate seed germination, while others inhibit this process or even kill the seed embryo. Differences also exist in hardness and permeability of the seed coat of different weed species at which species of Chenopodiaceae and Leguminosae are good examples on hard seed coat species. These characters cause differences in germination and growth of seedlings and may confer another cause of herbicide resistance. Avoidance of herbicide toxicity may result from seed interring into dormancy and not further responding to the applied herbicide with no absorption or translocation of the herbicide into the embryo. In addition, herbicide molecules may be deactivated or degraded inside the seed itself by some oxidative enzymes or may bound into certain constituent inside the seed. On the other hand, stimulation of weed seeds to germinate using certain herbicides also exists and allows higher seedling emergence and partitioning of herbicide molecules among individuals of weed species. Division of herbicide molecules among the high number of emerged seedlings would further dilute herbicide inside weed plants. All the above mentioned factors should be considered when herbicide resistance is discussed. These may cause great differences in weed seed germination, seedling growth patterns, and distribution in the field. Seed germination rate was often more rapid for herbicide-resistant *Echinochloa oryzicola* Vasing. than for herbicide-susceptible seeds, implying greater dormancy in the latter. Germination rate was often more rapid for herbicide-resistant than for herbicide-susceptible seeds, implying greater dormancy in the latter [61]. Population shift in life cycle has been previously discussed as shown by *Senecio vulgaris* L. in order to avoid herbicide phytotoxicity. Scursoni et al. [62] have shown that seeds from *Avena fatua* plants that had survived the application of diclofop-methyl in barley crops had a lower dormancy level. Moreover, an anticipated emergence timing of *A. fatua* was detected in plots that had been treated with diclofop-methyl the previous year in relation to the emergence timing observed in plots that had not been treated with the herbicide.

12. Factors enhance seed germination and dormancy breaking

Dormancy is synchronized to the environment by a complex regulatory system. This is directed by the balance between the dormancy-promoting (abscisic acid) and dormancy-releasing (gibberellins) hormones via both hormone levels and sensitivity. Seed dormancy is a survival mechanism underlying the life cycle strategies of plants by controlling the seasonal timing of germination in the natural environment.

Weed species differ widely in seed dormancy and longevity, season in which they emerge and grow, depth from which they can emerge, and seed responsiveness to light and other germination stimuli. Weed seeds that remain dormant in the soil often germinate in response to changes in temperature, moisture, oxygen, or light.

Overcoming seed dormancy may be easily achieved under laboratory conditions through a number of practices/treatments including seed hand scarification, rubbing and peel/cortex/extra structure removal, alternate temperature, chemical treatments, and dipping/soaking seed in water (legumes) or could be changed by scarification—with acids or microbes, rubbing on a sandpaper or pricking it with a pin or needle. As an example, *Rhynchosia capitata* (Heyne ex Roth) DC. seeds exhibit physical dormancy that is mainly due to the impermeability of their coat. Mechanical scarification and acid scarification (soaking of seeds in H_2SO_4 for 60 and 80 min and in HCl for 12 and 15 h) were very effective in breaking dormancy and enhancing germination [63]. Dormancy can be also overcome by alternate treatments of wetting and drying aiming to destroy the hard seed coat. In addition, seeds may be frozen and then dissolved, exposed to cold temperature and stratification, or washed by water for removal of inhibitors. Seed germination of *Eclipta prostrata* (L.) L. was completely inhibited in the dark, but in the dark/light, it was 93% at 20/30°C alternating day/night temperature. Germination was more than 80% at 140°C followed by incubation at 30/20°C for 14 days but declined at higher ratio until zero germination at 200°C. Germination is tolerant to salinity but highly sensitive to water stress. Seeds germinate at pH of 4–10 and are enhanced closure to soil surface but reduced thereafter until no germination obtained from a depth of 0.5 cm [64].

A novel method that overcomes coat-imposed dormancy has been reported by Tiryaki and Topu [65]. In their method, seeds were stored at −80°C for certain period and then treated immediately with hot water of 90°C for 5 s. This approach of freeze-thaw scarification provided 84 and 75% germination compared with 3 and 26% of *Lupinus albus* L. and *Trifolium pratense* L., respectively. In other cases genetic-controlled dormancy may not possibly overcome by physical or mechanical treatments as for seeds of *Nicandra physaloides* (L.) Gaertn. which possess one pair of iso-chromosomes. The presence or absence of an iso-chromosome determines whether a seed will germinate readily (2n = 20) or is dormant (2n = 19). *Echinochloa oryzicola* dormancy is possibly relieved through stratification. Stratification temperatures, moisture levels, and durations contributed to its seed dormancy released by decreasing hydrotime required for germination and by eliminating any germination sensitivity to oxygen [61]. Alternating temperatures nearly doubled germination rate in all weed populations of this species. Stratification at Y = 0 MPa increased germination rate compared to stratification at lower water potentials. Maximum germination rate occurred after 2–4 weeks of stratification at 0 MPa; it was suggested that field soil saturation in winter would contribute toward *E. oryzicola* dormancy release and decrease the time to seedling emergence.

Phleum paniculatum Huds. seeds had a shallow dormancy (20–30 d) when stored at room temperature (25 ± 5°C). Seeds could germinate at constant temperatures between 10 and 25°C. Light was not essential for seed germination, and pH values from 4 to 10 did not inhibit germination. Seeds were moderately adaptable to water potential and NaCl concentration, and germination rates decreased by 50% when water potential was −0.4 MPa or NaCl concentration was 130 mM. Increased soil burial depth decreased the seedling emergence, and no seeds emerged at depth more than 4 cm [66].

Cold stratification may be a highly selective treatment and hence did not decrease dormancy for any of *Lamium* species collected in Sweden, while warm stratification (21°C) of seed batches of all species that germinated when fresh increased dormancy but decreased over time for all tested species. Pretreatment with dry storage was most efficient in reducing dormancy for all annual *Lamium*. In contrast to cold or warm stratification, dry storage led to germination in darkness for all species [67]. Warm stratification increased germination, both in darkness and at 15/5°C, but did not cause germination of any of the two *Papaver aculeatum* populations tested at 30/20°C. Cold stratification reduced germination and limited germination to the cooler temperatures. Alternating cold and warm stratifications showed that the species undergoes dormancy cycles [23].

Seed dormancy of *Polygonum persicaria* L., *Chenopodium album*, *Spergula arvensis*, and *Sisymbrium officinale* (L.) Scop. [68] is regulated by field temperature and not nitrate and light. *Aciphylla glacialis* F. Muell. ex Benth seeds possess physiological dormancy that is overcome by cold stratification. Seeds have undeveloped embryos at dispersal but grow to germinate after 4–9 weeks at both constants 5°C and 10–5°C (day-night) temperatures. The species exhibits morphophysiological dormancy at which final percentage germination and dormancy status varied significantly among natural populations [69]. In another study Rhie et al. [70] reported that warm stratification (25/15°C) stimulated embryo growth and germinated the seeds of bamboo (*Nandina domestica* Thunb.), but cold stratification (5°C) was not required. Warm stratification at a constant 20°C speeds seed germination more than a fluctuating temperature at 25/15°C and shortened germination time by 4 months compared with that under natural conditions. Gibberellic acid (GA_3) at 100 and 1000 mg L^{-1} could substitute for warm stratification and break dormancy in seeds incubated at 15/6°C. In addition seeds may be exposed to light for chemical changes inside the seed or can be treated chemically with germination stimulants such as potassium nitrate, gibberellic acid, cytokinins, and auxins.

In the field, many agronomic practices affect weed seed dormancy and germination through their effects on the microenvironmental and edaphic conditions surrounding the seeds in the soil. Light penetration, soil water content, soil fertility, and temperature are modified by tillage, planting, harvesting, and other production practices that enhance or prevent weed seed germination. Changes in these environmental factors may modify indirectly phytohormone concentrations during seed development, which can subsequently affect dormancy status of the mature seed [3, 71].

It has been postulated that temperature is the only factor that directly influences the dormancy state of seeds, although the effects of other factors such as nitrate and light cannot be excluded [72]. Germination is influenced by factors such as temperature, light, nitrate, gaseous environment of the seed, and moisture content. Light appears as the most suited factor to influence in the field to enhance weed control. The behavior of weed seeds, in terms of dormancy characteristics, can be substantially different according to the location of the seed in the soil. Much of this response is related to a phytochrome requirement for germination, specifically, to the interconversions between the active (P_{fr}) and inactive (P_r) forms while the physiological mechanism involved in this conversion is poorly understood.

The changes in dormancy and germination of *Chenopodium album* L., *Polygonum persicaria* H., *P. lapathifolium* L. subsp. *lapathifolium*, *Sisymbrium officinale* (L.) Scop, and *Spergula arvensis* L. found regulated by temperature. Soil moisture and nitrate content had no effect. Germination of *C. album*, *S. officinale*, and *S. arvensis* was stimulated by light, nitrate, and desiccation. These factors all increased the width of the range of temperatures over which germination could proceed and therefore affected the expression of dormancy. Germination depended on the one hand on the actual field temperature after exhumation and on the range of the germination temperature, which was determined by the dormancy status of the seeds and soil temperature during burial. When nitrate was added during the test, the germination temperature range became wider, and germination could occur during a longer period of the year [73].

Karimmojeni et al. [74] studied dormancy breaking in seeds of *Thlaspi arvense* L., *Descurainia sophia* (L.) Webb ex Prantl., and *Malcolmia africana* (L.) W.T. Aiton (Brassicaceae) and reported that burying seeds of *D. sophia*, at a depth of 10 cm for 60 days, resulted in 55% germination and seeds dry-stored at 20°C for 180 days (45%) showed the highest level of germination. In *M. africana*, the germination percentage reached 95% when seeds buried at a depth of 1 cm were soaked in a GA_3 concentration of 150 ppm. *T. arvense* had the lowest level of germination compared to the other species. The highest percentage of *T. arvense* germination was obtained in seeds treated with 150 ppm GA_3. Potassium nitrate partly increased germination of *M. africana*, which initially was less dormant than those of *T. arvense* and *D. sophia*. Light is the most common germination trigger, though many seeds also respond to temperature and moisture fluctuations, increased aeration, and increased release of nitrate and other soluble nutrients that occur in tilled soil [75]. Tillage may end dormancy stage by exposing seeds to temperature and light. In many weed species, dormancy may be ended by treatment with a single factor or a mixture of ecological factors such as exposure to cold or humid conditions or to cold temperature and light.

In certain species cracking of the hard seed coat resulted from its exposure to mechanical pressure through coldness, freezing, scarification, or abrasion or through microbial attack that is necessary for germination. In other species seed coat must be destroyed, modified, or partially dissolved to provide the embryo with the necessary secondary growth factors. Embryos that are constrained by a mechanical barrier, such as the surrounding endosperm, perisperm, or megagametophyte (such as those that exhibit coat-enhanced dormancy), appear to require a weakening of these structures to permit radicle protrusion. This weakening involves partial enzymatic degradation of the cell walls. Seeds of *Datura ferox* exhibit increased endo-p-mannanase and p-mannosidase activities in the micropylar region of the endosperm after red light stimulation and many hours before the radicle protrudes through it [76]. Sometimes it is necessary washing the inhibitory chemicals. In other cases humid cold period or stratification is required during autumn and late in winter.

Certain species such as wild oats will not germinate unless seeds are exposed to warm dry conditions for dormancy breaking. Many weed species require light for seed germination, and this occurs when they get mature or may be stimulated by seed burying in the soil. Therefore, one effect of tillage is through dormant seed exposure for red light even for a short time to enhance germination. Some researchers study the implementation of tillage during the night to prevent stimulation of seed germination of certain weed species. The ratio of the active phytochrome far-red (P_{fr}) and inactive phytochrome red (P_r) determines whether the seed is dormant or not. The optimum ratio is established after exposure of the seed to white light which converts P_r to P_{fr} in the embryo. Outer coverings form a filter to high incident light on the seed and modify its effectiveness in converting P_r to P_{fr}. *Chenopodium album* seeds with dark seed coats are less responsive to light than their thin, light-coated counterparts. Dark seeds filter out light and reduce the conversion of P_r to P_{fr} when exposed to light; hence they remain dormant for longer periods than thin light-coated seeds.

In general, the main factors inducing or ending seed dormancy are light including day length, light type, dark period, and photoperiod; immature embryo; impermeable seed coat to water, oxygen, or both as in seeds of *Amaranthus* spp., *Capsella bursa-pastoris*, and wild *Brassica*.; and chemical inhibitors such as ABA and allelochemicals. Oxygen of percentages in the soil ranged between 1 and 9%. CO_2 with a percentage between 5 and 15%, temperature. Low oxygen prevents oxidative stress and germination, while high CO_2 induced dormancy of *Brassica alba* seeds. The after-ripening needs which are irrelevant to the degree of the embryo maturation are also involved in dormancy due to physiological changes that are not very well understood.

Soil disturbance and light stimulate germination and emergence prior to crop planting in order to remove as many weeds from the soil seed bank as possible. However, weed seed banks can be manipulated [75] by encouraging seed germination or trapping them to germinate, modifying their environment, placing seeds in a position that are not able from or in others where they are much exposed to heat and light, and using certified crop seeds.

A dense, shading plant canopy can also deepen the dormancy in some weed seeds. The dim green light under such a canopy can actually be more effective than continuous darkness in inhibiting the germination of light-responsive seeds [77]. Light quality under such foliage may have rendered weed seeds more dormant [78]. Dense crop canopies may also reduce subsequent weed emergence by reducing seed production or increasing seed mortality and hence provide favorable habitat for seed predators, resulting from reductions in the seed bank and subsequent weed emergence [79]. This dormancy strategy works best for annual weeds whose seeds often show conditional, light-mediated dormancy. Drought and shade were found to reduce reproductive allocation and resulted in seed of *Avena fatua* with less intense primary dormancy than the plants grown under resource-rich conditions, but had no apparent effect on seed vigor [80].

Karrikinolide may be an efficient means of stimulating weed seeds to germinate. These weed seeds would otherwise remain viable in the weed seed bank. Karrikinolide appeared to stimulate a broad spectrum of weed species, including wild turnip, wild radish, wild mustard, wild oat, cape weed, barley grass, and Paterson's curse. Germination stimulation of weed seeds was dependent on seed dormancy state, with some species (i.e., wild turnip and barley grass) responding differently depending on seed maturity conditions in the maternal environment. The application of karrikinolide at relatively low rates (2 g/ha) to weeds both *ex situ* and *in situ* can significantly improve weed seed germination while lower rates were inefficient. Karrikinolide seems working as a germination stimulant rather than a dormancy-breaking agent [81]. The smoke-derived chemical karrikinolide responses of seeds differed among populations of *Brassica tournefortii*, but this variation was reduced when seeds developed in a common environment. The KAR1 responses of each population changed when seeds developed in different environments. Different parental environments affected germination responses of the populations differently, showing that parental environment interacts with genetics to determine KAR1 responses. Seeds from droughted plants were 5% more responsive to KAR1 and 5% less dormant than seeds from well-watered plants, but KAR1 responses and dormancy state were not intrinsically; however, the parental environment in which seeds develop is one of the key drivers of the KAR1 responses of seeds [82].

13. Parasitic weeds and seed germination stimulants and inhibitors

13.1 Germination stimulants

Natural chemicals may include seed germination and growth stimulants including those for parasitic weeds. The ability of these chemicals to modify or break down seed dormancy and physiologically activate food transport, and embryo growth and development, or ruling out the over wintering stage of different living organisms, defense mechanisms, parasitic plants attachment and historian invasion to host tissues are examples on their positive effects [83].

Several natural chemicals have been identified as seed germination stimulants of parasitic species [84]. The main groups are the sesquiterpene lactones [85, 86]; some are alectrol from *Vigna sinensis* L., orobanchol from *Trifolium pratense* [87], and strigolactones and orobanchol from sorghum [88, 89]. Strigol was identified from the root exudates of *Gossypium hirsutum* L. plants and *Zea mays* L., which all are also produced by *Striga* host plants [90]. Some sesquiterpene lactones induce seed germination of *Orobanche cumana* Wallr. [91] better than the synthetic germination stimulant, GR24. However, Rice [39] stated that the stimulatory effect of allelochemicals is rather very limited or even rare and usually associated with low concentration effects of the compounds.

Strigol, alectrol, and sorgolactone are *Striga* germination stimulants, all produced by the parasite host plants, while different plant species have shown a strong ability to stimulate seed germination of different *Orobanche* species by more than 90% [90]. Ethylene was reported by Zehar and Fer [92] to induce germination of GR24-conditioned seeds of *Orobanche ramosa*, and its synthesis is required for parasite germination. However, a large number of synthetic substances were reported to stimulate germination of *Striga* species, among which are coumarin derivatives, scopoletin, thiourea, allylthiourea, sulfuric acid, sodium hypochlorite, and inositol [93]. Thidiazuron herbicide has been reported to activate ethylene release [94] and thus indirectly enhance *Striga* seed germination, although it is regarded by the same author as an inhibitor of haustorial development.

Ethylene- and ethephon-releasing compounds were effective in stimulating *Striga asiatica* (L.) Kuntze [95], while under field conditions, it was highly efficient against *Striga hermonthica* (Del.) Benth. Other chemicals have been found to stimulate *Striga* germination *in vitro* including several growth hormones and kinetins. Thuring et al. [96] were able to synthesize two diastereomers of demethylsorgolactone. Nijmegen-1 was active at low concentration as a suicidal germination agent for both *Striga* and *Orobanche* [97]. Yoneyama et al. [98] reported that jasmonates and related compounds elicited seed germination of *O. minor* and methyl jasmonate was the most active stimulant on several *Striga* and *Orobanche* species. The synthetic germination stimulants, strigol analogues (GR compounds), stimulate seed germination of different *Striga* and *Orobanche* species. Strigol has been reported for *Orobanche* stimulation [99], and its analogues GR7 and GR45 stimulated germination of *O. minor*.

Luque et al. [100] reported that parthenolide and 3,5-dihydroxydehydrocostus lactone significantly increased *O. cumana* germination and exhibited higher activity than GR24. The positive role of this hormone was further confirmed. The activity of germination stimulants for suicidal germination of *Orobanche* seeds under field conditions could be substantially enhanced by applying brassinolide (2a, 3a, 22R, and 23R-tetrahydroxy-24Smethyl-B-homo-7-oxa-5-a-cholesten-6-ono) and related compounds to the infested soils [101].

The role of microorganisms (e.g., *Streptomyces*) has also been implicated in *Orobanche* seed germination. Christeva and Naumova [102] reported different strains of *Streptomyces* to induce germination of *O. ramosa* and concluded that microorganisms may take part in germination processes of this parasite. In another study, Yoneyama et al. [103] reported stimulation of *O. minor* seed germination by certain fungal metabolites including cotylenins and fusicoccins at concentrations as low as 10^{-5} M and up to more than 50%.

Different plant species have been reported to show a strong ability to stimulate seed germination of different *Orobanche* species by more than 90%, and extracts of hundreds of plant species were tested for possibly stimulating or inhibiting seed germination of different *Orobanche* spp.; many proved effective and may be considered as trap, cover, and catch species or a source of natural germination stimulants for these parasites [104–106].

13.2 Germination inhibitors

Inhibitory allelochemicals may work at different stages of the parasite's life cycle from germination to growth and development. However, a reverse action may be obtained at low concentration received by the parasite.

Serghini et al. [107] reported that coumarins affect the normal growth and development of *Orobanche cumana* seedlings and the effect was more intense from the resistant than in the susceptible cultivars. Coumarins (ayapin and scopoletin) from sunflower plants were implicated as inhibitory allelochemicals to germination; growth and development of O. *cumana* [91] are both excreted by sunflower roots into the environment and could act as toxic allelochemicals to the parasite [108]. Bar-Nun and Mayer [109] reported the presence of large amounts of oleic and linoleic acids and small amounts of stearic and palmitic acids in *Orobanche aegyptiaca* (Pers.) Pomel. seeds. The authors expected these acids to interfere with sugar metabolism and thus prevent parasite seed germination during the preconditioning period. Sunflower seeds treated with 40 ppm of benzo(1,2,3)thiadiazole-7-carbothioic acid S-methyl ester (BTH) for 36 h completely prevented infection of *O. cumana* in root chambers [110]. In pot studies, at considerable inoculums of O. *cumana* seeds, the total number of parasite shoots was reduced by almost 90% with 60 ppm of BTH. Different *Fusarium* spp. were reported by Sauerborn [111] to infect *Orobanche* and *Striga* seeds and parasite plants, and he emphasized the role of phytotoxins in the process. He added that members of the genus *Fusarium* produce toxins such as enniatin, fumonisin, fusaric acid, moniliformin, and trichothecenes that possess a broad range of biological activities and metabolic effects. However, some of these compounds have been already proposed and considered to be used as natural herbicides [112]. Later studies showed fusaric acid and 9,10-dehydrofusaric acid to be active at low doses in reducing *Striga* seed germination [113]. Zehar and Fer [92] found T-2 toxin from *Fusarium* sp. to be the most active among 14 fungal toxins tested, inhibiting 100% seed germination at 10^{-5} M and was active down to 10^{-7} M (19% inhibition). Deoxynivalenol [vomitoxin], produced by *Fusarium* spp., was also very effective, causing 100 and 69% reduction in germination when assayed at 10^{-4} and 10^{-5} M, respectively. The high activity shown by some fungal toxins suggests that they may have potential as more natural and safe herbicides to suppress *S. hermonthica* seed germination. The use of toxic secondary metabolites could represent a useful alternative strategy in the management of parasitic weeds, by interfering with the induced germination process, and that fungal culture extracts could be an interesting source of new compounds acting as natural and original herbicides on these parasites.

Ancymidol, uniconazole, and paclobutrazol were reported as strong inhibitors of *Orobanche ramosa* germination, and CCC, daminozide, and prohexadione at 10^{-5} had a similar effect [92]. The inhibitory effect of paclobutrazol and uniconazole could be resulted from the increased level of abscisic acid.

Oxidative metabolism of ABA into phaseic acid and exogenous ABA is a strong inhibitor of *O. ramosa* germination [89]. Germination of *S. asiatica* was reduced by silver thiosulphate and COCH, inhibitors of ethylene action, and ACC oxide [114]. Aminoethoxyvinyl glycine reduced cytokinin thidiazuron-induced parasite germination.

14. Genetic studies on weed seed dormancy

Seed dormancy is mainly found in wild species in which weeds form the integral part of these species and are facing extreme challenges under field conditions. Dormancy is a strategy of weed survival and persistence that challenge farmers under all conditions. In contrast, crops lack such a trait and always show rapid and uniform seed germination [6] with some exceptions as for cereals that possess a moderate degree of dormancy to resist preharvest sprouting (the germination of seeds after maturation but before harvest in moist environment) that results in substantial yield loss. Dormancy is a genetically complex trait controlled by polygenes, but its effects are influenced by the genetic background and environmental factors [115]. However, genotype-by-environment interactions have been reported for seed dormancy in different species [116, 117]. The growth environment greatly affects both the number and the influence of individual quantitative trait locus (QTL) in a mapping population [118]. Gu et al. [119] suggested the presence of genetically complex networks in the regulation of variation for seed dormancy in natural populations of weedy rice (*Oryza sativa*). Multiple loci and epistasis control genetic variation for seed dormancy in the weed. Iso-chromosomes have been also mentioned to determine seed germination and dormancy. However, molecular studies on dormancy genetics are clearly rare, and there is a need for research in this aspect and genetic dormancy differences among and between weed species and their populations and the link of these with environmental conditions.

15. Seed dormancy as a weed survival strategy

Dormancy is a property that enables weed seeds to survive conditions hazardous to plant growth, such as the periods of extreme heat and drought in certain geographical regions or the long cold winters in temperate regions, and allows them to germinate at some later time or in some other place [120, 121]. Similarly, Roberts [122] indicated that seed dormancy mechanisms tend to inhibit seed germinating at the wrong time and in the wrong place. Hence, weed seeds can persist in the soil for many years and germinate after experiencing conditions favorable for seedling survival through maturity [120]. Such a behavior results in the accumulation of large quantities of seeds in the soil, forming either transient or persistent banks which constitute the regenerative strategy developed by many weed species [31, 120]. In further support of this concept, the analysis of the composition of most seed pools has revealed that dormant seeds are only produced in large numbers by species whose growing populations are subject to periodic local extinction, such as in the case of early succession. In addition, species exposed to elimination conditions such as the use of extensive applications of herbicides or implementation of certain other agricultural practices (flooding, soil solarization, deep tillage, and continued disturbance) tend to show tolerance or resistance to such practices and deep seed dormancy as a hazard avoidance strategy. Similar strategy is also expressed well under severe stress conditions such as extreme drought and salinity.

16. Conclusions

Seed dormancy is of different types and has several definitions; it is a highly complicated phenomenon weakly understood until now in spite of the huge number of publications available. The poor understanding of dormancy is mainly due the complexity of the factors involved including mechanical, physiological, and biochemical that may be also genetically and/or environmentally controlled. Although much is known on dormancy induction and breaking, but the complicated and interrelated issues occur in the seed itself including the seed coat, embryo, cotyledon, endosperm, cell organelles, nuclei, and associated structures that all need much research work on their roles and effects on dormancy. In addition, a similar work is required on the role and influence of the external environmental factors. Weeds are of most concern since possess different types of dormancy and challenges farmers as well as researchers under field conditions. Literature on the causal factors of dormancy are huge and varied including information on the seed coat and its structures, effects of temperature, light and phytochrome system, hormones, synthetic chemicals, enzymes, temperature, O_2, CO_2, seed internal structures, embryo and its surrounding structures, inhibitors, cell membranes, secondary metabolites and allelochemicals, stresses, agricultural practices and genetics, soil moisture and relative humidity, salinity, soil pH, and many other related factors. These factors and their interactions influence seed dormancy and germination. The interaction between environmental factors and seed factors that determines seed germination time, periodicity, sequences and percentages and the final density of the emerged weed population. However, while researchers all over the world are trying to solve and reveal the secrecy stands behind seed dormancy in order to find solutions for some problems that the farmers facing under field conditions at which seed dormancy of weeds is the main issue, dormancy from the weedness perspectives is a survival strategy that these unwanted plant species adapt themselves to survive and exist free from hazards and insure their generations and genetic lines. Therefore dormancy is a natural phenomenon created through genetics, environment, or their interactions, while research work carried out till now is just to understand this trial and to accommodate ourselves accordingly with. Therefore, seed dormancy is one of the most important adaptive mechanisms in plants, which protects seeds from precocious germination in the presence of the inappropriate conditions for growth continuation.

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References

[1] Islam AKMM, Yeasmin S, Qasem JRS, Juraimi AS, Anwar MP. Allelopathy of medicinal plants: Current status and future prospects in weed management. Agricultural Sciences. 2018;**9**:1569-1588. DOI: 10.4236/as.2018.912110

[2] Grundy AC. Predicting weed emergence: A review of approaches and future challenges. Weed Research. 2003;**43**:1-11

[3] Dyer WE. Exploiting weed seed dormancy and germination requirements through agronomic practices. Weed Science. 2017;**43**(3):498-503. DOI: 10.1017/S0043174500081534

[4] Schatral A, Osborne JM. Germination and dormancy states of seeds in the environmental weed *Rumex vesicarius* (Polygonaceae). I. Seed polymorphism and germination of extracted seeds. Australian Journal of Botany. 2006;**54**(8):773-782. DOI: 10.1071/BT04201

[5] White DE. Physiological adaptations in two ecotypes of canada thistle *Circium arvense* (L.) Scop [MSc thesis]. Davis, USA: University of California; 1979

[6] Altieri MA, Liebman MZ. Weed Management in Agroecosystems: Ecological Approaches. Boca Raton: CRC Press; 1988

[7] Batlla D, Benech-Arn RL. Predicting changes in dormancy level in weed seed soil banks: Implications for weed management. Crop Protection. 2007;**26**:189-197

[8] Vleeshouwers LM. Modelling weed emergence patterns [Ph.D. thesis]. Wageningen, The Netherlands: Agricultural University; 1997

[9] Benech-Arnold RL, Sanchez RA, Forcella F, Kruk BC, Ghersa CM. Environmental control of dormancy in weed seed banks in soil. Field Crop Research. 2000;**67**:105-122

[10] Mayer AM, Poljakoff-Mayber. The Germination of Seeds. 3rd ed. Oxford: Pergamon Press; 1982. 211 pp

[11] Chavarria PL. Seed dormancy characteristics in six weed species as affected by after-ripening temperatures and field conditions. Retrospective theses and dissertations. 8062 [Ph.D thesis]. Ames, Iowa: Iowa State University; 1986. Available from: https://lib.dr.iastate.edu/rtd/8062

[12] Nikolaeva MG. Factors controlling the seed dormancy pattern. In: Khan AA, editor. The Physiology and Biochemistry of Seed and Germination. Amsterdam, The Netherlands: Elsevier/North-Holland Biomedical Press; 1977. pp. 51-74

[13] Venier P, Funes G, Garcia C. Physical dormancy and histological featuresof seeds of five Acacia species (Fabaceae) from xerophytic forests in central Argentina. Flora. 2012;**207**:39-46

[14] Gama-Arachchige N, Baskin J, Geneve R, Baskin C. Identification and characterization of ten new water gaps in seeds and fruits with physical dormancy and classification of water-gap complexes. Annals of Botany. 2013;**112**:69-84

[15] Black M, Bewley J, Halmer P. The Encyclopaedia of Seeds: Science, Technology and Uses. London: CABI; 2006

[16] Sm'ykal P, Vernoud V, Blair MW, Soukup A, Thompson RD. The role of the testa during development and in establishment of dormancy of the legume seed. Frontiers in Plant Science. 2014;**5**:1-19

[17] Rodrigues-Junior A, Faria J, Vaz T, Nakamura A, Jose A. Physical

dormancy in *Senna multijuga* (Fabaceae: Caesalpinioideae) seeds: The role of seed structures in water uptake. Seed Science Research. 2014;**24**:147-157

[18] Cardina J, Sparrow DH. Temporal changes in velvetleaf (*Abutilon theophrasti*) seed dormancy. Weed Science. 2017;**45**(1):61-66. DOI: 10.1017/S0043174500092481

[19] Robles-Díaza E, Floresb J, Yáñez-Es, L. Paths of water entry and structures involved in the breaking of seed dormancy of Lupinus. Journal of Plant Physiology. 2016;**192**:75-80

[20] Brown NAC, Bridglall SS. Preliminary studies of seed dormancy in *Datura stramonium*. Souh Africa Journal of Botany. 1987;**53**(1):107-109

[21] Qasem JR. Aqueous extract effect of nettle-leaved goosefoot (*Chenopodium murale*) on wheat and barley. Research Journal of Aleppo University. 1990;**14**:37-53

[22] Malavert C, Batllaa D, Benech-Arnolda RL. Temperature-dependent regulation of induction into secondary dormancy of *Polygonum aviculare* L. seeds: A quantitative analysis. Ecological Modelling. 2017;**352**:128-138

[23] Karlsson LM, Milberg P. Seed dormancy pattern and germination preferences of the South African annual *Papaver aculeatum*. South African Journal of Botany. 2007;**73**:422-428

[24] Dahlquist RM, Prather TS, Stapleton JJ. Time and temperature requirements for weed seed thermal death. Weed Science. 2007;**55**:619-625

[25] Simpson GM. Seed Dormancy in Grasses. Cambridge, UK: Cambridge University Press; 1990

[26] Carrera E, Holman T, Medhurst A, Dietrich D, Footitt S, Theodoulou FL, et al. Seed after-ripening is a discrete developmental pathway associated with specific gene networks in Arabidopsis. Plant Journal. 2008;**53**:214-224

[27] Finch-Savage WE, Leubner-Metzger G. Seed dormancy and the control of germination. New Phytologist. 2006;**171**:501-523

[28] Koornneef M, Karssen CM. Seed dormancy and germination. In: Koornneef M, Karssen CM, editors. Arabidopsis. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press; 1994. pp. 313-334

[29] Leopold AC, Glenister R, Cohn MA. Relationship between water content and afterripening in red rice. Physiologia Plantarum. 1988;**74**:659-662

[30] Kołodziejek J, Patykowski J. The effect of temperature, light and calcium carbonate on seed germination and radicle growth of the polycarpic perennial *Galium Cracoviense* (Rubiaceae), a narrow endemic species from southern Poland. Acta Biologica Cracoviensia Series Botanica. 2015;**57**(1):70-81. DOI: 10.1515/abcsb-2015-0006

[31] Karssen CM. Seasonal patterns of dormancy in weeds seeds. In: Khan AA, editor. The Physiology and Biochemistry of Seed Development, Dormancy and Gennination. Amsterdam, The Netherlands: Elsevier/North-Holland Biomedical Press; 1982. pp. 243-270

[32] Egley GH. Seed germination in soil: Dormancy cycles. In: Kigel J, Galili J, editors. Seed Development and Germination. New York: Marcel Dekker, Inc.; 1995. p. 853

[33] Hillhorst HWM. The regulation of secondary dormancy. The membrane hypothesis revised. Seed Science Research. 1998;**8**:77-90

[34] Taab A. Seed dormancy and germination in solanum nigrum

and *S. physalifolium* as influenced by temperature conditions [Doctoral thesis]. Uppsala: Swedish University of Agricultural Sciences; 2009. 48 pp

[35] Kołodziejek J, Patykowski J. Effect of environmental factors on germination and emergence of invasive *Rumex confertus* in Central Europe. The Scientific World Journal. 2015;**2015**:170176. DOI: 10.1155/2015/170176

[36] Arc E, Sechet J, Corbineau F, Rajjou L, Marion-Poll A. ABA cross talk with ethylene and nitric oxide in seed dormancy and germination. Frontiers in Plant Science, Plant Cell Biology. 2013;**4**:1-19. DOI: 10.3389/fpls.2013.00063

[37] Karssen CM. Two sites of hormonal action during germination of *Chenopodium album* seeds. Physiologia Plantarum. 1976;**36**:264-270

[38] Rezvani M, Zaefarian F, Amini V. Effects of chemical treatments and environmental factors on seed dormancy and germination of shepherd's purse (*Capsella bursa-pastoris* (L.) Medic.). Acta Botanica Brasilica. 2014;**28**(4):495-501. DOI: 10.1590/0102-33062014abb3337

[39] Rice EL. Allelopathy. 11th ed. London: Academic Press; 1984

[40] Bouteau HE-M, Bailly C. Oxidative signaling in seed germination and dormancy. Plant Signaling & Behavior. 2008;**3**(3):175-182. DOI: 10.4161/psb.3.3.5539

[41] Finch-Savage WE, Footitt S. Seed dormancy cycling and the regulation of dormancy mechanisms to time germination in variable field environments. Journal of Experimental Botany. 2017;**68**(4):843-856. DOI: 10.1093/jxb/erw477

[42] Koller D. Environmental control of seed germination. In: Kozlowski TT, editor. Seed Biology. Vol. II. New York: Academic Press; 1972. pp. 1-101

[43] Menegat A, Milberg P, Nilsson ATS, Andersson L, Vico G. Soil water potential and temperature sum during reproductive growth control seed dormancy in *Alopecurus myosuroides* Huds. Ecology and Evolution. 2018;**8**:7186-7194

[44] Menge EO, Bellairs SM, Lawes MJ. Seed-germination responses of *Calotropis procera* (Asclepiadaceae) to temperature and water stress in northern Australia. Australian Journal of Botany. 2016;**64**(5):441-450. DOI: 10.1071/BT16044

[45] Xiong RC, Ma Y, Wu HW, Jiang WL, Ma XY. Effects of environmental factors on seed germination and emergence of velvetleaf (*Abutilon theophrasti*). Planta Daninha. 2018;**36**. Epub Oct 29, 2018. DOI: 10.1590/s0100-83582018360100122

[46] Bochenek A, Golaszewski J, Piotrowicz-Cieslak AI, Gorecki RJ. The effects of temperature on the dormancy and germination of *Cirsium arvense* (L.) Scop. seeds. Acta Societatis Botanicorum Poloniae. 2009;**78**(2):105-114

[47] Fei H, Tsang E, Cutler AJ. Gene expression during seed maturation in Brassica napus in relation to the induction of secondary dormancy. Genomics. 2007;**89**:419-428

[48] Cici SZH. Maternal environment modulates dormancy and germination in *Vaccaria hispanica*. Agrotechnology. 2017;**6**:154. DOI: 10.4172/2168-9881.1000154

[49] Humphries T, Chauhan BS, Florentine SK. Environmental factors effecting the germination and seedling emergence of two populations of an aggressive agricultural weed; *Nassella trichotoma*. PLoS One. 2018;**13**(7):e0199491. DOI: 10.1371/journal.pone.0199491

[50] Orlovsky N, Japakova U, Zhang H, Volis H. Effect of salinity on seed germination, growth and ion content in dimorphic seeds of Salicornia europaea L. (Chenopodiaceae). Plant Diversity. 2016;**38**:183-189

[51] Soltani E, Baskin CC, Baskin JM, Soltani A, Galeshi S, Ghaderi-far F, et al. A quantitative analysis of seed dormancy and germination in the winter annual weed *Sinapis arvensis* (Brassicaceae). Botany. 2016;**94**(4):289-300. DOI: 10.1139/cjb-2015-0166

[52] Teasdale JR, Pillai P. Contribution of ammonium to stimulation of smooth pigweed (*Amaranthus hybridus* L.) germination by extracts of hairy vetch (*Vicia villosa* Roth) residue. Weed Biology and Management. 2005;**5**:19-25. DOI: 10.1111/j.1445-6664.2005.00155.x

[53] Brainard DC, Tommaso AD, Mohler CL. Intraspecific variation in germination response to ammonium nitrate of *Amaranthus powellii* originating from organic versus conventional vegetable farms. Weed Science. 2006;**54**:435-442. DOI: 10.1614/WS-05-162R1.1

[54] Qasem JR. Chemical control of *Prosopis farcta* (Banks and Sol.) Macbirde in the Jordan Valley. Crop Protection. 2007;**26**:572-575

[55] Vleeshouwers L, Bouwmeester H, Karssen C. Redefining seed dormancy: An attempt to integrate physiology and ecology. Journal of Ecology. 1995;**83**:1031-1037

[56] Hawkins KK, Allen PS, Meyer SE. Secondary dormancy induction and release in *Bromus tectorum* seeds: The role of temperature, water potential and hydrothermal time. Seed Science Research. 2017;**27**:1-14. DOI: 10.1017/S0960258516000258

[57] Putwain PD, Scott KR, Holliday RJ. The nature of resistance to traizine herbicides: Case histories of phenology and population studies. In: Le Baron HM, Gressel J, editors. Herbicide Resistance in Plants. New York: John Wiley & Sons; 1982. p. 99

[58] Harper JL. Population Biology of Plants. London: Academic Press; 1977

[59] Bewley JD, Black M. Physiology and Biochemistry of Seeds in Relation to Germination, Viability, Dormancy and Environmental Control. Vol. 2. New York: Springer-Verlag; 1982. 375 pp

[60] Abbaspour R, Cici SZH, Dogaheh MA, Abbaspour N. Effect of fertilizer application and irrigation on germination of Jimson weed (*Datura stramonium* L.) as a medicinal plant. International Journal of Medical Research & Health Sciences. 2016;**5**(S):377-380

[61] Boddy LG, Bradford KJ, Fischer AJ. Stratification requirements for seed dormancy alleviation in a wetland weed. PLoS One. 2013;**8**(9):e71457. DOI: 10.1371/journal.pone.0071457

[62] Scursoni JA, Benech-Arnold RL, Hirchoren H. Demography of wild oat in barley crops: Effect of crop, sowing rate and herbicide treatment. Agronomy Journal. 1999;**91**:478-485

[63] Ali HH, Tanveer A, Nadeem MA, Asghar HN. Methods to break seed dormancy of *Rhynchosia capitata*, a summer annual weed. Chilean Journal of Agricultural Research. 2011;**71**(3):483-487

[64] Chauhan BS, Johnson DE. Influence of environmental factors on seed germination and seedling emergence of Eclipta (Eclipta prostrate) in a tropical environment. Weed Science. 2008;**56**:383-388

[65] Tiryaki I, Topu M. A novel method to overcome coat-imposed seed

dormancy in *Lupinus albus* L. and *Trifolium pratense* L. Journal of Botany. 2014;**2014**, Article ID 647469, 6 pages. DOI: 10.1155/2014/647469

[66] Wu H, Zhang P, Chen G, Pan L, Li J, Dong L. Environmental factors on seed germination and seedling emergence of *Phleum paniculatum* Huds. Chilean Journal of Agricultural Research. 2018;**78**(3):370-377. DOI: 10.4067/S0718-58392018000300370

[67] Karlsson LM, Milberg P. Variation within species and inter-species comparison of seed dormancy and germination of four annual *Lamium* species. Flora. 2008;**203**:409-420

[68] Bouwmeester HJ, Karssen CM. Annual changes in dormancy and germination in seeds of *Sisymbrium officinale* (L.). Scop. New Phytologist. 1993;**124**:179-191

[69] Hoyle GL, Cordiner H, Good RB, Nicotra AB. Effects of reduced winter duration on seed dormancy and germination in six populations of the alpine herb *Aciphyllya glacialis* (Apiaceae). Conservation Physiology. 2014;**2**:1-11

[70] Rhie YH, Kim J, Lee SY, Kim KS. Non-deep simple morphophysiological dormancy in seeds of heavenly bamboo (*Nandina domestica* Thunb.). Scientia Horticulturae. 2016;**210**:180-187

[71] Skubacz A, Daszkowska-Golec A. Seed Dormancy: The Complex Process Regulated by Abscisic Acid, Gibberellins, and Other Phytohormones that Makes Seed Germination Work. IntechOpen; 2017. DOI: 10.5772/intechopen.68735. Available from: https://www.intechopen.com/books/phytohormones-signaling-mechanisms-and-crosstalk-in-plant-development-and-stress-responses/seed-dormancy-the-complex-process-regulated-by-abscisic-acid-gibberellins-and-other-phytohormones-th

[72] Riemens MM, Scheepens PC, van der Weide RY. Dormancy, Germination and Emergence of Weed Seeds, with Emphasis on the Influence of Light. Vol. 2004. Wageningen: Plant Research International B.V.; 2004. pp. 1-26

[73] Bouwmeester HJ. The Effect of Environmental Conditions on the Seasonal Dormancy Pattern and Germination of Weed Seeds. Wageningen, The Netherlands: Agricultural University in Wageningen, Department of Plant Physiology, Arboretumlaan 4, NL-6703 BD Wageningen, The Netherlands and Department of Vegetation Science, Plant Ecology and Weed Science; 1990

[74] Karimmojeni H, Taab A, Rashidi B, Bazrafshan AH. Dormancy breaking and seed germination of the annual weeds *Thlaspi arvense*, *Descurainia sophia* and *Malcolmia africana* (Brassicaceae). Journal of Plant Protection Research. 2014;**54**(2):179-187

[75] Brainard D, Mohler C, Schonbeck M. Manipulating weed seed banks to promote their decline. Extension; Organic Agriculture. 2013. Available at: https://articles.extension.org/pages/18528/manipulating-weed-seed-banks-to-promote-their-decline [Accessed: May 15, 2019]

[76] Sánchez RA, de Miguel L. Phytochrome promotion of mannan-degrading enzyme activities in the micropylar endosperm of *Datura ferox* seeds requires the presence of the embryo and gibberellins synthesis. Seed Science Research. 1997;**7**:27-33

[77] Mohler CL. Weed life history: Identifying vulnerabilities. In: Liebman M et al., editors. Ecological Management of Agricultural Weeds. New York: Cambridge University Press; 2001. pp. 40-98

[78] Martens K, Martens M. Weed control in row crops. In: Oral

Presentation, Pennsylvania Association for Sustainable Agriculture Conference; Feb. 7-9 2008; State College, PA. 2008

[79] Davis A, Liebman M. Cropping systems effects on giant foxtail (*Setaria faberi*) demography: 1. Green manure and tillage timing. Weed Science. 2003;**51**:919-929. DOI: 10.1614/P2002-133A

[80] Gallagher RS, Granger KL, Snyder Am, Pittmann D, Fuerst EP. Implications of environmental stress during seed development on reproductive and seed bank persistence traits in wild oat (*Avena fatua* L.). Agronomy. 2013;**3**:537-549. DOI: 10.3390/agronomy3030537

[81] Dixon K. Releasing agricultural weed seed dormancy through application of a novel smoke derived chemical. In: Final Report. Botanic Garden and Parks Authority, West: Grains Research & Development Corporation, Australian Government; 2005

[82] Gorecki MJ, Long RL, Flematti GR, Stevens JC. Parental environment changes the dormancy state and karrikinolide response of Brassica tournefortii seeds. Annals of Botany. 2012;**109**:1369-1378. DOI: 10.1093/aob/mcs067. Available online at: www.aob.oxfordjournals.org

[83] Qasem JR. Parasitic weeds and allelopathy, from the hypothesis to the proof. In: Reigosa MJ, Pedrol N, Gonzalez L, editors. Allelopathy, A Physiological Process with Ecological Implications. The Netherlands: Springer; 2006. pp. 565-637

[84] Zwanenburg B, Reizelman A. En route to the isolation and characterization of the strigolactone receptor using biotin labelled strigolactone analogues. In: Fer A, Thalouam P, Joel DM, Musselman LI, ParkerC,VerkleijJAC,editors.Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France: Faculté des Sciences, Université de Nantes; 2001. pp. 102-105

[85] Butler LG. Chemical communication between the parasitic weed Striga and its crop host. A new dimension in allelochemistry. In: Inderjit, Dakshini KMM, Einhellig FA, editors. Allelopathy: Organisms. Processes and Applications. Washington, DC: ACS Symposium Series 582. American Chemical Society; 1995. pp. 389. pp. 158-168

[86] Denev I, Pereira A, Verstappen F and Bouwmeester H. Biosynthesis of *Orobanche* germination stimulants. In Fer A, Thalouarn P, Joel DM, Musselman LJ, Parker C, Verkleij JAC (eds) Proceedings of the 7th International Parasitic Weed Symposium. 2001. pp. 110-113. Nantes, France: Faculté des Sciences, Université de Nantes; DOI: 10.2478/jppr-2014-0028

[87] Sugimoto Y. Germination stimulants for the seeds of root parasitic weeds. Journal of Pesticide Science. 2000;**25**:438-440

[88] Yokota T, Sakai H, Okuno K, Yoneyama K, Takeuchi Y. Alectrol and orobanchol, gennination stimulants for *Orobanche minor*, from its host red clover. Phytochemistry. 1998;**49**:1967-1973

[89] Yoneyama K, Takeuchi Y, Yokota T. Natural gennination stimulants for Orobanche minor. In: Fer A, Thalouam P, Joel DM, Musselman LI, ParkerC,VerkleijJAC,editors.Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France; 2001. p. 123

[90] Wegmann K. The *Orobanche* problem in tobacco. In: Wegmann K, Musselman LJ, Joel DM, editors. Current Problems of Orobanche Research. Proceedings of the Fourth International

Workshop on Orobanche. Albena, Bulgaria; 1998. pp. 21-24

[91] Perez-de-Luque A, Rubiales D, Galindo GC, Macias FA, Jorrin J. Allelopathy and allelochemicals within the plant-parasitic weed interaction. Studies with the *sunflower-Orobanche cumana* system. In: Fer A, Thalouam P, Joel DM, Musselman LI, ParkerC,VerkleijJAC,editors.Proceedings of the 7'hInternational Parasitic Weed Symposium. France: Nantes; 2001. pp. 196-199

[92] Zehar N, Fer A. Gennination of Orobanche ramosa is controlled by gibberellins and ethylene. In: Fer A, Thalouam P, Joel DM, Musselman L, ParkerC,VerkleijJAC,editors.Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France: Faculté des Sciences, Université de Nantes; 2001. p. 122

[93] Worsham AD, Egley GH. Physiology of witchweed seed donnancy and gennination. In: Sand PF, Eplee RE, Westbrooks RG, editors. Witchweed Research and Control in the United States. Champaign, USA: Weed Science Society of America; 1990. pp. 11-26

[94] Babiker AGT, Parker C, Suttle JC. Induction of *Striga* seed germination by thidiazuron. Weed Research. 1992;**32**:243-248

[95] Egley GH. Ethylene stimulation of weed seed germination. Agriculture and Forestry Bulletin, University of Alberta. 1982;**5**:13-18

[96] Thuring JWFW, Heinsman NWJT, Jacobs RWAWM, Nefkens GHL, Zwanenburg B. Asymmetric synthesis of all stereoisomers of demethylsorgolactone. Dependence of the stimulatory activity of *Striga hermonthica* and *Orobanche crenata* seed gennination on the absolute configuration. Journal of Agriculture and Food Chemistry. 1997;**45**:507-513

[97] Wigchert SCM, Kuiper E, Boelhouwer G, Nefkense GHL, Verkleij JA, Zwanenburg B. Dose-response of seeds of the parasitic weeds *Striga* and *Orobanche* toward the synthetic germination stimulants GR24 and Nijmegen I. Journal of Agriculture and Food Chemistry. 1999;**47**:1705-1710

[98] Yoneyama K, Ogasawara M, Takeuchi Y, Konnal M, Sugimoto Y, Sassa T, et al. Effect of jasmonates and related compounds on seed germination of *Orobanche minor* Smith and *Striga hermonthica* (Del.) Benth. Bioscience, Biotechnology and Biochemistry. 1998;**62**:1448-1450

[99] Vail SL, Dailey OO Jr, Connik W, Peppennan AB. Strigol synthesis and related structurebioactivity studies. In: Thompson A, editor. The Chemistry of Allelopathy. Biochemical Interactions among Plants, American Chemical Society Symposium Series 268. Washington, DC, USA: American Chemical Society; 1985. pp. 445-456

[100] deLuqueAP,GalindoJCG,MaciasFA, Jorrin J. Sunflower sesquiterpene lactone models induce *Orobanche cumana* seed germination. Phytochemistry. 2000;**53**:45-50

[101] Takeuchi Y, Omigawa Y, Ogasawara M, Yoneyama K, Konnai M, Wosham AD. Effects of brassinosteroids on conditioning and germination of clover broomrape (*Orobanche minor*) seeds. Plant Growth Regulator. 1995;**16**:153-160

[102] Christeva T, Naumova S. Stimulation of broom rape seed germination by soil microorganisms. In: Wegmann K, Musselman LJ, Joel DM, editors. Current Problems of Orobanche Researches. Proceedings of the Fourth International Workshop on Orobanche. Albena, Bulgaria: Institute for wheat and sunflower "Dobroudja"; 1998. pp. 73-77

[103] Yoneyama K, Takeuchi Y, Ogasawara M, Konnal M, Sugimoto Y, Sassa T. Cotylenins and fusicoccins stimulate seed germination of *Striga hermonthica* (Del.) Benth and *Orobanche minor* Smith. Journal of Agriculture and Food Chemistry. l998;**46**:1583-1586

[104] Babaei S, Alizadeh H, Jahansouz MR, Mashhadi HR, Moeini MM. Management of *Phelipanche aegyptiaca* Pomel. using trap crops in rotation with tomato (*Solanum lycopersicon* L.). Australian Journal of Crop Science (AJCS). 2010;**4**(6):437-442

[105] Ma YQ, Zhang W, Dong SQ, Ren XX, An Y, Lang M. Induction of seed germination in *Orobanche* spp. by extracts of traditional Chinese medicinal herbs. Science China Life Sciences. 2012;**55**:250-260. DOI: 10.1007/s11427-012-4302-2

[106] Qasem JR. Branched broomrape (*Orobanche ramosa* L.) control in tomato (*Lycopersicon esculentum* Mill.) by trap crops and other plant species in rotation. Crop Protection. 2019;**120**:75-83

[107] Serghini K, Perez de Luque A, Castejon-Munoz M, Garcia-Torres L, Jorrin JV. Sunflower (*Helianthus annuus* L.) response to broomrape (*Orobanche cernua* Loefl.) parasitism: Induced synthesis and excretion of 7-hydroxylated simple coumarins. Journal of Experimental Botany. 2001;**52**:2227-2234

[108] Guitierrez-Mellado MC, Edwards R, Tena M, Cabello F, Serghini K, Jorrin J. The production of coumarin phytoalexins in different plant organs of sunflower (*Helianthus annuus* L.). Journal of Plant Physiology. 1995;**l49**:261-266

[109] Bar-Nun N, Mayer AM. Composition of and changes in storage compounds in *Orobanche. aegyptiaca* seeds during preconditioning. Journal of Plant Sciences. 2002;**50**:277-279

[110] Sauerborn J, Buschmann H, Ghiasi KG, Kogel KH. Benzothiadiazole activates resistance in sunflower (*Helianthus annuus*) to the root-parasitic weed *Orobanche cumana*. Phytopathology. 2002;**92**:59-64

[111] Sauerborn J. Angiospennous root parasites and fungi as natural antagonists. In: Fer A, Thalouam P, Joel DM, Musselman LI, Parker C, Verkleij JAC, editors. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France: Faculté des Sciences, Université de Nantes; 2001. pp. 248-251

[112] Strobel GA, Kenfield D, Bunkers Q, Sugawara F, Clardy J. Phytotoxins as potential herbicides. Experientia. 1991;**47**:819-826

[113] Zonno MC, Vurro M. Effect of fungal toxins on germination of *Striga hermonthica* seeds. Weed Research. 1999;**39**:15-20

[114] Gabbar A, Babiker T, Buttler LG, Ejeta G, Woodson WR. Enhancement of ethylene biosynthesis and germination by cytokinins and 1-aminocyclopropane-I-carboxylic acid in *Striga asiatica* seeds. Physiologia Plantarum. 1993;**89**:21-26

[115] Anderson JA, Sorrells ME, Tanksley SD. RFLP analysis of genomic regions associated to pre-harvest sprouting in wheat. Crop Science. 1993;**33**:453-459

[116] Paterson AH, Sorrells ME. Inheritance of grain Upadhyay, M. P., and G. M. Paulsen, 1988. Heritabilities and gedormancy in white-kernelled wheat. Crop Science. 1990;**30**:25-30

[117] Upadhyay MP, Paulsen GM. Heritabilities and dormancy in white-kernelled wheat. Crop Science. 1988;**30**:25-30

[118] Groos C, Gay G, Perretant MR, Gervais L, Bernard M, et al. Study

of the relationship between pre-harvest sprouting and grain color by quantitative trait loci analysis in a white x red grain bread-wheat cross. Theoretical and Applied Genetics. 2002;**104**:39-47

[119] Gu X-YG, Kianian SF, Foley ME. Multiple loci and epistases control genetic variation for seed dormancy in weedy rice (*Oryza sativa*). Genetics. 2004;**166**:1503-1516

[120] Fenner M. Seed Ecology. New York: Chapman and Hall; 1985. 151 pp

[121] Tran VN, Cavanagh AK. Structural aspects of dormancy. In: Murray DR, editor. Seed Physiology, Germination and Reserve Mobilization. Vol. II. Sydney, Australia: Academic Press; 1984. pp. 1-44

[122] Roberts EH. The interaction of environmental factors controlling loss of dormancy in seeds. Annals of Applied Biology. 1981;**98**:552-555